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Recent evidence of biological recovery from acidification in the Adirondacks (New York, USA): a multiproxy paleolimnological investigation of Big Moose Lake

Kristina M.A. Arseneau, Charles T. Driscoll, Lindsay M. Brager, Karen A. Ross, and Brian F. Cumming

Abstract: This investigation provides evidence of biological recovery from acidification in an acid-impacted Adirondack (New York, USA) lake. Water chemistry measurements collected monthly since 1982 show that Big Moose Lake is undergoing chemical recovery from acid deposition. To assess possible biological recovery, changes in chrysophyte, diatom, and cladoceran assemblages are analyzed in a sediment core. Three questions are addressed: (*i*) is there a significant shift in species composition after the 1995 implementation of the US Acid Rain Program? (*ii*) Are post-1995 changes in species composition consistent with chemical recovery from acidification or, rather, other changing chemical/climatic factors? (*iii*) Are the species assemblages returning to their pre-acidification state? Post-1995 declines in the relative abundance of diatom and chrysophyte taxa with low pH-optima and increases in taxa with higher pH-optima indicate biological recovery from acidification. In contrast, the cladocera remain unresponsive to post-1995 increases in pH. No species group has returned to its pre-disturbance state and post-ca. 1995 increases in certain taxa (e.g., *Synura echinulata*) may be related to recent climate warming in the Adirondacks.

Résumé : Notre recherche apporte des preuves de la récupération biologique de l'acidification dans un lac affecté par l'acidité dans les Adirondacks (New York, É.-U.). Des données de chimie de l'eau récoltées à chaque mois depuis 1982 montrent que le lac Big Moose connaît un rétablissement chimique des effets des précipitations acides. Afin d'évaluer la possibilité d'un rétablissement biologique, nous avons analysé les changements dans les peuplements de chrysophytes, de diatomées et de cladocères dans une carotte de sédiments. Nous posons trois questions: (*i*) est-ce que la mise en vigueur du programme américain sur les pluies acides (U.S. Acid Rain Program) en 1995 a entraîné un changement significatif dans la composition des espèces? (*ii*) Les changements observés après 1995 correspondent-ils au rétablissement chimique après l'acidification ou plutôt à la modification d'autres facteurs chimiques/climatiques? (*iii*) Les associations d'espèces retournent-elles à leur état d'avant l'acidification? Le déclin après 1995 de l'abondance relative des taxons de diatomées et de chrysophytes à pH optimum bas et l'augmentation des taxons à pH optimum plus élevé indiquent un rétablissement biologique de l'acidification. En revanche, les cladocères ne répondent pas à l'augmentation de pH depuis 1995. Aucun des groupes d'espèces n'a retrouvé son état d'avant la perturbation; les augmentations de certains taxons (en particulier, *Synura echinulata*) peuvent être dues à un réchauffement climatique récent dans les Adirondacks.

[Traduit par la Rédaction]

Introduction

Acid deposition, a by-product of fossil fuel combustion, has severely impacted aquatic ecosystems across North America and Europe. Acidification (i.e., a decline in lakewater pH and acid neutralizing capacity) typically results in a simplification of aquatic foodwebs as acid-sensitive species

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are extirpated from the system (Baker and Christensen 1991). Declining lake-water pH can also lead to increases in monomeric aluminum concentrations and water clarity (Munson et al. 1990). Additionally, long-term exposure to acid precipitation can lead to depletion of available calcium in watershed soils, altering the export of calcium to nearby waterbodies over time (Likens et al. 1996).

The detrimental effects of acid deposition prompted the United States government to implement the 1990 Clean Air Act Amendments (CAAA). A goal of Title IV of the 1990 CAAA was to decrease sulphur dioxide and nitrogen oxide emissions, which contribute to the production of acid deposition (Driscoll et al. 2001). As of 2003, the United States has seen a 50% decline in sulphur dioxide emissions below their levels in 1973 (Jenkins et al. 2007). Much of these declines followed the 1995 implementation of the Acid Rain Program (ARP), a market-based "cap and trade" system regulated by the United States Environmental Protection Agency (USEPA 2009). Since the implementation of the ARP, regional surveys of lake-water chemistry have demonstrated a widespread decline in lake-water sulphate concentrations, but increases in acid neutralizing capacity (ANC) and pH are less commonly documented (Jeffries et al. 2003; Skjelkvåle et al. 2005; Driscoll et al. 2007).

One area that has exhibited widespread chemical recovery from acidification is the Adirondack region of New York State. Many Adirondack lakes are acid-sensitive, as much of the region is characterized by thin glacial-till soils underlain by granitic bedrock with limited ability to neutralize acid deposition (Driscoll et al. 1991). As such, many Adirondack lakes acidified under high sulphate deposition regimes, with some of the most acid-sensitive lakes acidifying in the early 1900s (Cumming et al. 1992*b*, 1994). More recently, a survey of 48 long-term monitoring sites in the Adirondacks found that 65% of the lakes showed increases in pH and 77% showed increases in ANC from 1992 to 2004 (Driscoll et al. 2007). However, to date, little work has been done to assess whether or not chemical recovery from acidification in the Adirondacks has resulted in biological recovery.

In the Adirondacks, biological recovery is expected to follow chemical recovery in acid-impacted areas and be characterized by an increase in the abundance of acid-sensitive taxa and a decline in the abundance of acid-tolerant taxa as lake-water pH increases (Driscoll et al. 2001). The onset of biological recovery typically lags behind the onset of chemical recovery, although the length of lag-period varies between taxonomic groups (e.g., 1–6 years, Frost et al. 2006) and between lakes. Delays in biological recovery may be due to several factors, including the lake's chemical status (e.g., persistent metal contamination, Graham et al. 2007), delays in species colonization events (e.g., Keller and Yan 1998), altered predation (e.g., Nilssen and Wævågen 2002) or competition regimes (e.g., Binks et al. 2005), and (or) other changing environmental factors (e.g., climate warming, Tropea et al. 2010).

Various studies have employed a range of metrics to define targets for biological recovery (Gray and Arnott 2009). For example, some studies have defined recovery based on the results of experimental acidification studies (e.g., Findlay 2003; Turner et al. 2009) or on a set of reference lakes that are believed to be representative of a geographic region (e.g., Yan et al. 1996; Keller et al. 2002). Other studies have designated site-specific targets based on paleolimnological reconstructions (e.g., Tropea et al. 2010).

Paleolimnology uses the chemical, physical, and biological characteristics of lake sediments to infer the environmental histories of lakes (Smol 2008). In the paleolimnological literature, the target for biological recovery has been traditionally defined as a return to a lake's pre-disturbance condition (i.e., the condition of the species assemblages prior to acidification). However, other factors such as long-term changes in land use should be taken into account when designating a pre-disturbance (or reference) condition for a particular lake (Renberg et al. 2009, Norberg et al. 2010).

Previous paleolimnological studies have examined the influence of acid deposition on North American lakes (Charles et al. 1990; Dixit et al. 1992) as well as evidence for biological recovery from acidification (Majewski and Cumming 1999; Ginn et al. 2007*b*; Tropea et al. 2010). In the Adirondacks, the remains of siliceous algae such as diatoms (Heterokontophyta, Bacillariophyceae) and scaled chrysophytes (Heterokontophyta, Chrysophyceae and Synurophyceae) in sediment cores have previously been used to infer changes in lake-water pH since pre-industrial times (Charles et al. 1990; Cumming et al. 1994). Likewise, previous paleolimnological studies have investigated the impact of acidification on aquatic invertebrates such as cladoceran zooplankton (Arthropoda, Branchiopoda) (Paterson 1994). The effects of acidification on cladoceran taxa may be of particular interest, as members of the genus *Daphnia* are calcium-sensitive and may be negatively impacted by declines in lake-water calcium concentrations (Ashforth and Yan 2008; Jeziorski et al. 2008).

The goal of this investigation was to assess whether or not biological recovery has followed chemical recovery in an acid-impacted Adirondack lake, using paleolimnological techniques. To provide a comprehensive assessment of biological recovery, three questions are addressed: (*i*) Has there been a significant shift in species composition in the diatom, chrysophyte, and cladoceran assemblages since the 1995 implementation of the Acid Rain Program? (*ii*) If so, are the recent (ca. 1995–2007) changes in species composition consistent with chemical recovery from acidification (i.e., increase in pH and (or) decline in monomeric aluminum) or, rather, other changing chemical and climatic factors? And finally, (*iii*) are the recent (ca. 1995–2007) species assemblages returning to a community composition similar to their pre-disturbance state?

Only those assemblages (diatoms, chrysophytes, cladocera) that showed significant shifts in species composition since the 1995 implementation of the ARP (question 1) were examined in further detail in questions 2 and 3. We hope that this investigation will provide insight into the recovery trajectories of organisms in acid-impacted lakes in the Adirondacks and elsewhere across North America.

Materials and methods

Study site

Big Moose Lake (43°49′02″N, 74°51′23″W) is a large (surface area, 515 ha; maximum depth, 22 m), thin-till, intensively studied drainage lake located in the southwestern por-

tion of Adirondack Park (New York, USA) (Charles et al. 1987). A detailed history of Big Moose Lake is provided in Charles et al. (1987) and Barlow (2004). Briefly, the first camp on Big Moose Lake was built in 1876. Disturbance in the watershed was minimal prior to the 1900s. Selective logging occurred in the watershed from 1895 to 1915. There was a forest fire in the watershed in 1903 and severe windstorms in 1938, 1950, and 1995. In 2002, there were an estimated 220 private residences near Big Moose Lake, not all of which had direct access to the waterfront (Barlow 2004). Recent measures of total phosphorus (TP) and chlorophyll *a* (Chl*a*) collected by the Adirondack Lakes Survey Corporation show that, in 2009, Big Moose Lake could be classified as an oligotrophic lake (TP, 4.7 $\mu g \cdot L^{-1}$) with low productivity (Chl*a*, 2.0 $\mu g \cdot L^{-1}$).

The main purpose of this investigation is to examine biological recovery from acidification. However, to contextualize any biological recovery patterns documented in Big Moose Lake, we provide a brief summary of the chemical recovery currently ongoing in the system. Long-term chemical monitoring data suggest that the lake is currently undergoing chemical recovery (Driscoll et al. 2003, 2007). The long-term trends in chemical and climatic variables for Big Moose Lake from 1982 to 2007 show declines in lake sulphate and nitrate concentrations since the mid-1990s (see Fig. 1). The decline in acid anion concentration has been coupled with increases in ANC and pH, as well as declines in total monomeric aluminum concentration. Since the mid-1990s, lake-water pH has rarely dropped below 5.0 and ANC has rarely dropped below 0, indicating that Big Moose Lake can no longer be considered chronically acidic. Lake-water calcium concentration has declined since the 1980s, whereas DOC has increased in concentration since the mid-1990s. Lastly, there appears to be little directional change in SiO_2 concentration, average monthly temperature, total monthly precipitation, or total monthly snowfall, though year-to-year variability is high.

In this investigation, analyses of possible biological recovery following chemical recovery were performed between two a priori defined time periods (period 1, 1983–1993; period 2, 1997–2007, see section on Statistical analyses for more detail). The mean values of each chemical/climatic variable in period 1 and period 2 are illustrated in Fig. 1, which also indicates whether the variable shows a significant difference in median between time periods (significance tested via Mann–Whitney *U* test, see Appendix A, Table A1, for test results). Mann–Whitney *U* test results show that the median concentration of acid anions, total monomeric aluminum, and calcium are significantly lower in period 2 than period 1. In contrast, the median pH, ANC, and DOC concentration is significantly higher in period 2 than period 1 (see Fig. 1 and Appendix A, Table A1).

Previous paleolimnological investigations have shown that Big Moose Lake acidified from a pre-industrial pH of approximately 5.8 to below 5.0 between approximately 1950 and the early 1980s (Charles et al. 1987; Cumming et al. 1994; Majewski and Cumming 1999). As Big Moose Lake acidified under relatively high sulphate and nitrate loads, it is expected to respond relatively rapidly to decreases in acid deposition (Cumming et al. 1994; Majewski and Cumming 1999). As the disturbance of the Big Moose Lake watershed was minimal prior to the 1900s, we have chosen to designate that time period as a pre-disturbance condition for the lake to serve as a recovery target.

Sediment collection and dating

A 34.5 cm sediment core was collected from the deepest basin of Big Moose Lake in 2007 using a Glew gravity corer (Glew 1989), equipped with a 7.6 cm (ID) core tube approximately 60 cm in length. Sediment cores were sectioned every 0.25 cm to yield a high-resolution stratigraphy. Sediment from each interval was stored in labelled Whirlpack® bags and transported in a cooler with ice to Queen's University (Kingston, Ontario) where the samples were stored in a cold room at 4 °C.

Twenty-one sediment intervals were chosen for gamma counting. Counting procedures followed the methods outlined in Schelske et al. (1994). Briefly, sediment intervals were dried overnight in a VirTis® Advantage freeze-dryer (SP Industries, Inc.). Dry sediment from each interval was placed in a labelled polypropylene tube and sealed with 2-Ton epoxy. The samples were stored at ambient temperature for at least 3 weeks until counted using a well-type germanium detector (Putnam Technology, Inc.) attached to a DSPEC digital gamma ray spectrometer. Sediment dates were calculated from unsupported ^{210}Pb activities using the CRS model and the computer program of Binford (1990). Calculated ^{210}Pb dates were fitted to an exponential curve to approximate the age-depth relationship in the stratigraphies of sedimentary species assemblages.

Microfossil enumeration

Diatom frustules and chrysophyte scales were enumerated on the same slides. Slide preparation followed the procedure outlined in Ginn et al. (2007*a*). Briefly, 0.2–0.3 g of wet sediment from each interval was transferred to a labelled glass vial to which approximately 20 mL of HNO_3–H_2SO_4 was added. Solutions were stirred, left overnight, and then put in a hot water bath (~80–85 °C) for approximately 6 h. The remaining solutions were rinsed 8–9× until a neutral pH was obtained (litmus test). Samples were plated as four 100% dilutions and dried overnight on a slide warmer. Cover slips were mounted on glass slides using Naphrax®.

Diatoms and chrysophytes were identified to the species or genus level. Chrysophytes that could not be identified using a light microscope were grouped into a broad taxonomic category *Mallomonas* "small" (Cumming et al. 1992*a*). Diatoms and chrysophytes were enumerated using a Leica DMR light microscope with oil-immersion objectives (numerical aperture = 1.3) at 1000× magnification. At least 400 diatoms and 500 chrysophytes were enumerated per slide.

Cladoceran samples were prepared following the procedure detailed in Korhola and Rautio (2001). Briefly, approximately 1.0 g of sediment was dissolved in 100 mL of 10% KOH solution and heated on a hot plate at 70–80 °C for 30 min. The remaining solution was sieved through a 38 μm sieve using deionized water, and the material captured by the sieve was transferred to labelled 15 mL glass vials. Two to three drops of safranin were added as a colorant, and seven to nine drops of 10% ethanol were added as a preservative. Samples were allowed to settle for at least 4 h before the solution in each vial was drawn down to a standard volume of

Fig. 1. Long-term (1982–2007) chemical and climatic monitoring data for Big Moose Lake. Chemical monitoring data for sulphate and nitrate (SO_4^{2-} + NO_3^-, μeq·L^{-1}), acid neutralizing capacity (ANC, μeq·L^{-1}), pH, total monomeric aluminum (Al, μmol·L^{-1}), calcium (Ca, mg·L^{-1}), dissolved organic carbon (DOC, μmol C·L^{-1}), and silicon dioxide (SiO_2, μmol·L^{-1}). Climatic monitoring data for average monthly temperature (T_{avg}, °C), total monthly precipitation (T_{precip}, cm), and total monthly snowfall (T_{snow}, cm). Grey boxes represent two time periods where biological recovery from acidification is examined (period 1, 1983–1993; period 2, 1997–2007). Horizontal grey lines represent the means of chemical/climatic variables measured in period 1 and period 2. Variables that show a significant difference in median between period 1 and period 2 via Mann–Whitney *U* test are denoted by an asterisk (*).

12 mL. Slides were prepared using 50 μL of well-mixed solution, and cover slips were mounted using a safranin–glycerine jelly medium. Cladoceran microfossils were identified at the species or the genus level. When possible, the post-abdominal claws of *Daphnia* were separated into the *Daphnia* cf. *pulex* and *Daphnia* cf. *ambigua* complexes (as per Witty 2004). *Ceriodaphnia* could not always be reliably distinguished from *D.* cf. *ambigua*, owing to the similarity of the two claw types (Nevalainen 2007), and so was included with the *D.* cf. *ambigua* counts. Overall, the fossil assemblages of Big Moose Lake were dominated by the *D.* cf. *pulex* group (average percent of daphniid collection, 97%).

Long-term (ca. 1780–2007) and short-term (ca. 1965–2007) stratigraphies of species relative abundance (the percent each species makes up in the entire species assemblage) were prepared for each indicator group, and included taxa that reached a relative abundance ≥ 5% at any point in the entire sediment chronology (ca. 1780–2007). Previous work has shown that one core from the deepest basin is sufficient to accurately represent the acidification history of Big Moose Lake (Charles et al. 1991), and that the counting variability in the relative abundance of diatoms/chrysophytes is low (± <2%, Charles et al. 1991). As such, changes in the relative abundance of species that are greater than counting variability are discussed below.

Diatom- and chrysophyte-inferred pH values were generated, hereinafter referred to as DI-pH and CI-pH, respectively. The DI-pH was inferred using all taxa that were in common with the northeastern North American (NENA) 494-lake training set (Ginn et al. 2007*a*) using the computer program C2 version 1.6.5 (build 1) (Juggins 2010). The DI-pH model is based on simple weighted-averaging with a square-root species transformation (Ginn et al. 2007*a*). The CI-pH was inferred using a modern chrysophyte dataset of 71 Adirondack drainage lakes using a weighted-averaging model with tolerance down weighting and a ln + 1 transformation (Cumming et al. 1994).

Statistical analyses

To identify whether a significant shift in species assemblages occurred after the 1995 implementation of the ARP (question 1), an analysis of similarities (ANOSIM) was applied to the subfossil assemblages. ANOSIM is a nonparametric analysis of rank similarities used to compare multivariate data between a priori defined groups (Clarke 1993). The test statistic, *R*, quantifies whether the average pair-wise similarity (i.e., Bray Curtis) within groups is greater than the average pair-wise similarity between groups. The significance of *R* is tested using a permutation test where the samples are randomly reshuffled between groups and *R* recalculated. If the original *R* is found to lie outside the 5% tail of the global distribution of *R*, the null hypothesis of no difference is rejected at an α of 0.05. A post-hoc test, known as the similarities percentage test (SIMPER), is used to identify which species make large (>%5) contributions to the difference in species composition seen between the two groups.

For Big Moose Lake, two 10 year time periods were identified a priori. Period 1 (ca. 1983–1993, mean pH = 5.14, ANC = –0.42 μeq·L^{-1}) is located prior to the 1995 enactment of the ARP and period 2 (ca. 1997–2007, mean pH = 5.54, ANC = 12.99 μeq·L^{-1}) is located after is enactment (see Fig. 1). If ANOSIM revealed a significant difference in species composition between time periods, the SIMPER post-hoc test was applied to assess which species were responsible for the changes and if the changes were consistent with biological recovery from acidification (i.e., a decrease in taxa with low pH optima, and an increase in taxa with a higher pH optima). ANOSIM and SIMPER were performed on untransformed species data using the program Primer version 6.1.11 (Primer-E. Ltd., Ivybridge, UK).

This statistical framework represents an attempt to identify periods when the lake was still acidic (period 1) versus a period following a measured increase in pH and ANC (period 2). The approach is conservative in that it recognizes that ^{210}Pb dating has errors that are difficult to quantify, and therefore may not allow direct comparisons between species assemblages (and specific taxa) with measured water chemistry. By delineating 10 year time periods and treating samples within each time period as replicates, major trends in the species assemblages can be identified.

Addressing questions 2 and 3 involved the use of direct and indirect ordination techniques, respectively. To identify if linear or unimodal ordination techniques were appropriate in this investigation, a Detrended Correspondence Analysis (DCA), scaled in standard deviation units, was applied (Jongman et al. 1995). If the length of the first axis is less than three standard deviation units, linear ordination techniques can be used to analyze the underlying data matrix (Lepš and Šmilauer 2003). DCA revealed that the length of the species turnover gradient for all indicators was short (i.e., <3 SD) and so linear ordination methods were applied.

If the ANOSIM detected a significant shift in species composition between the two a priori defined time periods, a Redundancy Analysis (RDA), a direct ordination technique, was used to assess whether the changes were consistent with chemical recovery from acidification (i.e., an increase in pH) or other chemical/climatic factors (question 2). In a RDA, the ordination axes constructed are constrained to be linear combinations of supplied environmental variables (Jongman et al. 1995). Species assemblage changes in Big Moose Lake from ca. 1983–2007 were constrained to measured chemical and climatic variables.

A limited number of chemical variables were selected for inclusion in the RDA to avoid spurious correlations. The

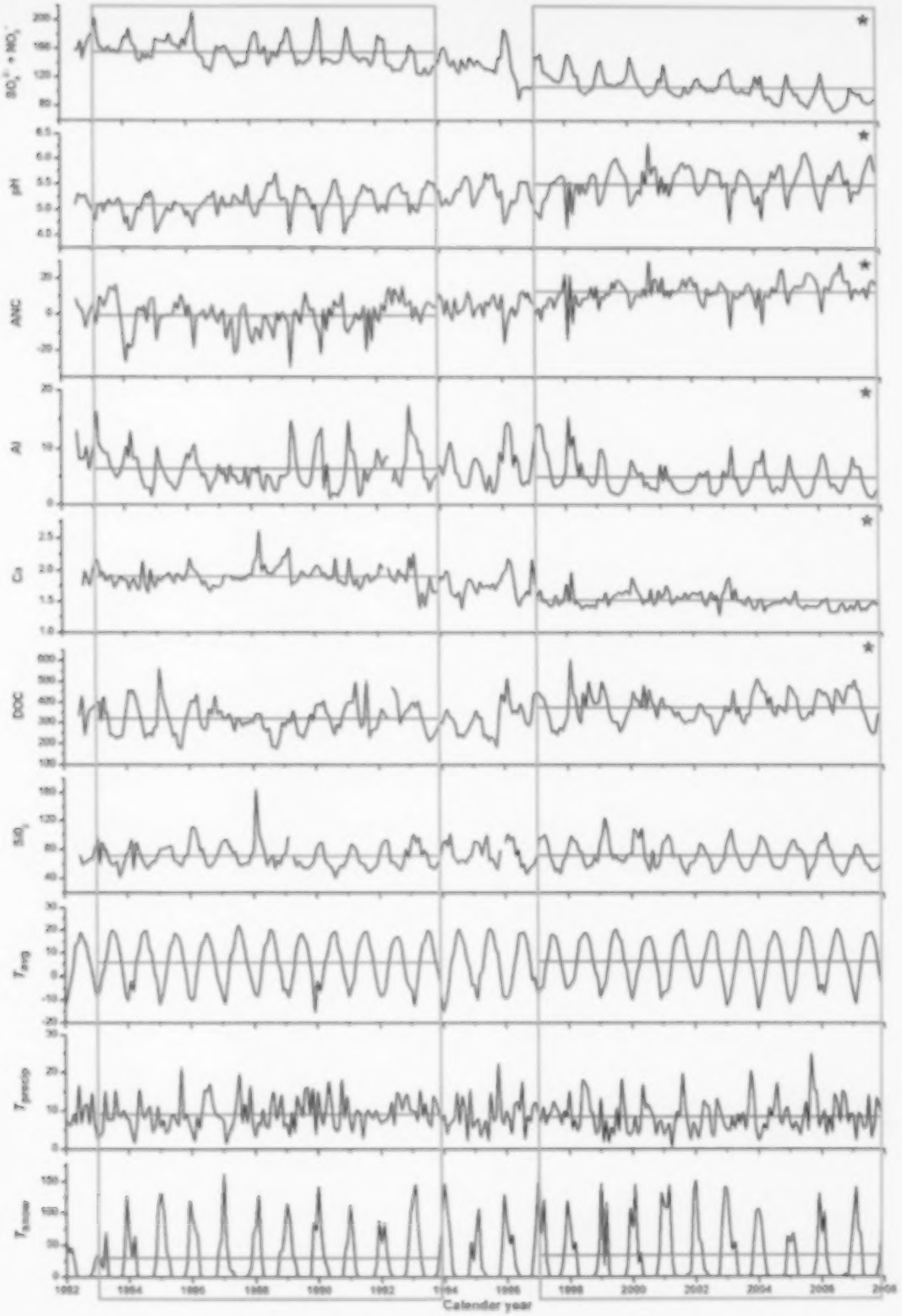
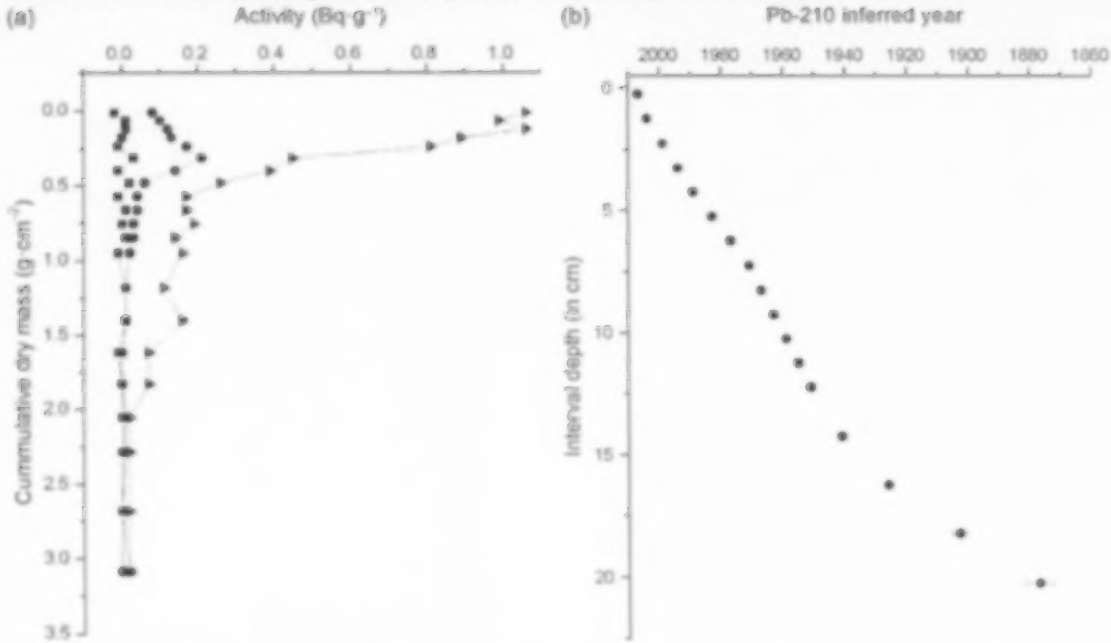

$SO_4^{2-} + NO_3^-$
pH
ANC
Al
Ca
DOC
SiO_2
T_{avg}
T_{precip}
T_{snow}
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
Calendar year

Fig. 2. (A) ^{210}Pb (filled triangle, ▶), ^{137}Cs (filled circle, ●), and ^{214}Bi (filled square, ■) activities (in disintegrations per second per gram dry sediment, Bq·g^{-1}) in a sediment core collected from Big Moose Lake in 2007. Activities are plotted against cumulative dry mass (g·cm^{-2}). (B) ^{210}Pb-inferred calendar year plotted against interval depth (cm). Error bars represent the standard errors.



chemical variables that were included are known to be important factors that contribute to the ecological distributions of diatom and chrysophyte taxa (see Siver 1991; Ginn et al. 2007*a*; Ginn et al. 2010), and included pH, total monomeric aluminum (Al, μmol·L^{-1}), DOC (μmol C·L^{-1}), and SiO_2 (Si, μmol·L^{-1}). All chemical variables used in this analysis were reported as yearly averages. Three general climatic variables were included in the RDA: mean annual temperature (°C), total annual precipitation (cm), and total annual snowfall (cm). Long-term temperature and precipitation records were available from 1895 to 2009 from the Wanakena weather station (44°08′53″N, 74°54′01″W), located approximately 35 km north-northwest of Big Moose Lake. Temperature and precipitation data were obtained from the United States Historical Climatology Network (UNSCN) and subjected to a suite of quality assurance measures (see Menne et al. 2009). Additionally, uncorrected monthly snowfall data were available from the National Climatic Data Center (NCDC). Snowfall records were collected from the Big Moose Lake SE station (43°48′N, 74°52′W), located approximately less than 5 km southeast of Big Moose Lake. Missing values in the 1983–2007 snowfall record were filled with the mean value over the 1931–2009 period (Lepš and Šmilauer 2003). A forward-selection procedure using Monte Carlo permutation tests was used to identify which environmental variables showed a significant relationship with the species data (Lepš and Šmilauer 2003). Environmental variables that were significant at $p \leq 0.1$ were used in the RDA. An α of 0.1 was chosen because small sample size ($n = 24$) increases the likelihood of committing a Type II error. Nonsignificant ($p > 0.1$) environmental variables were plotted passively in the ordination. RDA was performed using the computer program CANOCO version 4.5 (Plant Research International, Wageningen, the Netherlands).

Finally, Principal Components Analysis (PCA), a linear indirect ordination technique, was used to visually assess whether the recent (post-ca. 1995) species assemblages were returning to their pre-disturbance (pre-ca. 1900) condition (question 3). PCA is based on an implicit dissimilarity measure of Euclidean distance (Jongman et al. 1995). Sedimentary assemblages that are similar in species composition cluster closely in the ordination diagram. Thus, if recent (i.e., post-ca. 1995) species assemblages are found to cluster together with pre-disturbance (i.e., pre-ca. 1900) species assemblages in ordination space, present-day species assemblages are trending towards an ecological condition characteristic of pre-acidification times. Based on the known disturbance history of Big Moose Lake, species assemblages were divided in four a priori defined time periods for comparison: pre-ca. 1900 (pre-disturbance), ca. 1900 – pre-ca.1950 (early disturbance), ca. 1950 – ca. 1995 (acidification), and post-ca. 1995 – 2007 (post-ARP). PCA was performed using the computer program CANOCO version 4.5.

Results

Dating profiles

^{210}Pb activities were relatively high in Big Moose Lake and showed exponential decay with increasing core depth (see Fig. 2*a*). The unsupported ^{210}Pb showed an exponential decay with cumulative dry mass of sediment in the core. Beyond a depth of 20.5 cm, unsupported ^{210}Pb activity was equal to supported ^{210}Pb activity.

^{137}Cs typically binds poorly to the organic-rich sediment

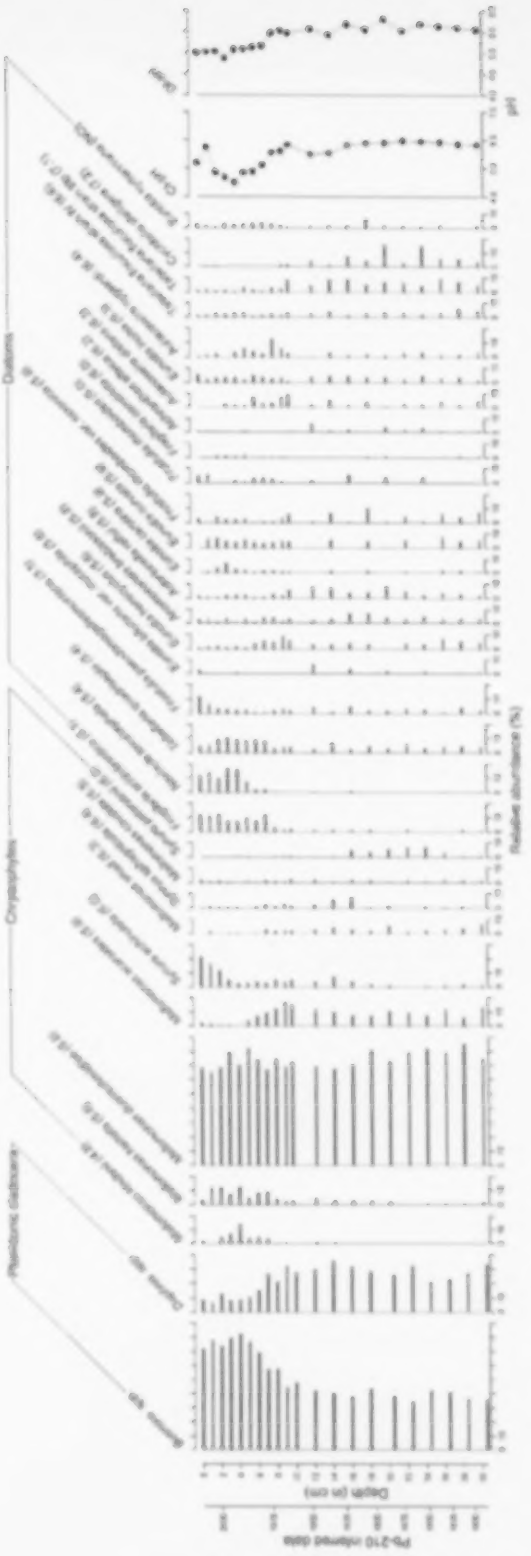


Fig. 3. Long-term (ca. 1780–2007) change in the relative abundance (%) of dominant (≥5%) planktonic cladocera, chrysophytes and diatom taxa in a ^{210}Pb-dated core from Big Moose Lake. Chrysophyte and diatom species are arranged by pH-optimum given in a 71-lake Adirondack calibration set (chrysophytes, Cumming et al. 1992*a*) and the northeastern North America (NENA) dataset (diatoms, Ginn et al. 2007*a*), respectively. Species not present in the NENA calibration set are demarked by NO (no-optimum). Chrysophyte-inferred pH (CI-pH) was inferred using a modern chrysophyte dataset of 71 Adirondack drainage lakes using a weighted-averaging model with tolerance down weighting and a ln + 1 transformation (Cumming et al. 1994). Diatom-inferred pH (DI-pH) is based on a weighted-averaging model with a square-root species transformation (Ginn et al. 2007*a*).

typical of Adirondack lakes (Heit and Miller 1987; Schelske et al. 1994). As such, estimates of calendar year were solely based on ^{210}Pb activities (see Fig. 2*b*). Standard errors of ^{210}Pb-inferred dates in the upper 14 cm (ca. 1950–present) were relatively low (± <1 year) and increased with core depth.

Long-term and short-term changes in species assemblages

A subdecadal, long-term (ca. 1780–2007) stratigraphy of all three species groups is provided (Fig. 3). Additionally, high-resolution short-term (ca. 1965–2007) stratigraphies are provided for diatoms, chrysophytes, and cladocera (Figs. 4, 5, and 6, respectively). The following sections summarize general trends in species composition for each group that appeared greater than expected counting variability (± <2%, Charles et al. 1991). In the following paragraphs, the pH optimum of each diatom (Ginn et al. 2007*a*) and chrysophyte (Cumming et al. 1992*a*) taxon is provided in brackets after its name.

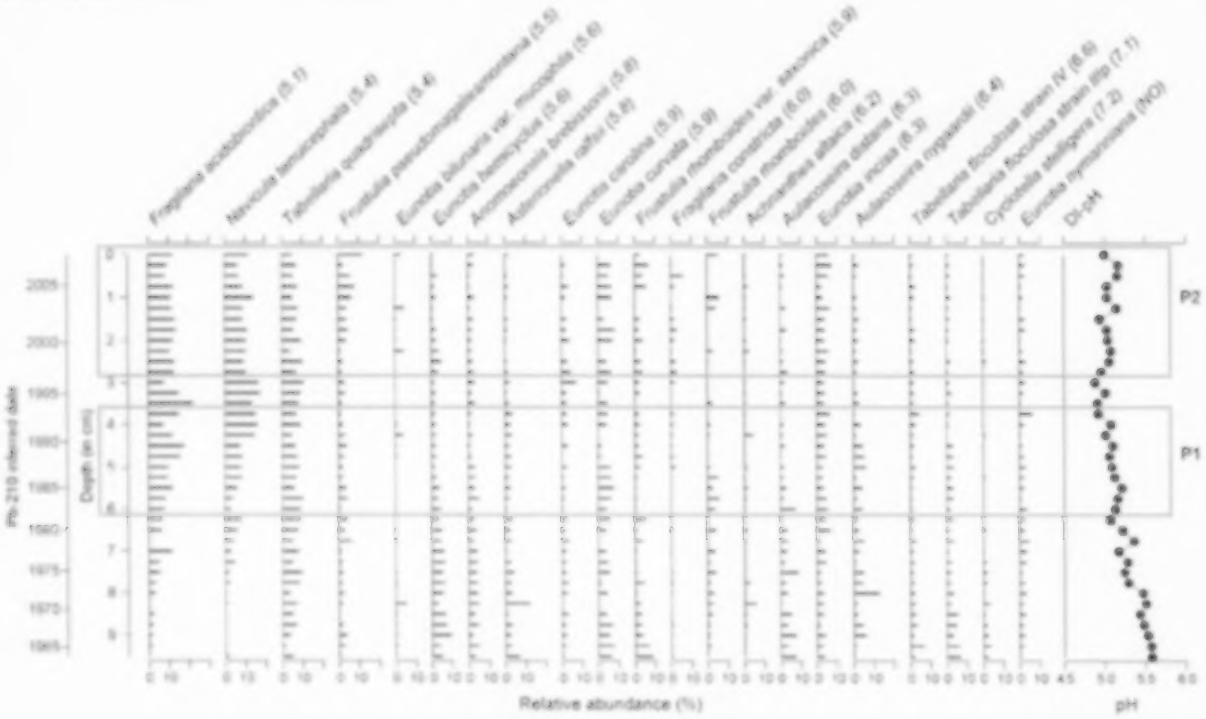
Diatoms

Long-term (ca. 1780–2007) changes in diatom relative abundance were similar to previously published work (Charles et al. 1990) (see Fig. 3). *Tabellaria flocculosa* strain IIIp (7.1) and *Cyclotella stelligera* (7.2) decline in relative abundance in the 1960s. The relative abundance of *Fragilaria acidobiontica* (5.1) and *Navicula tenuicephala* (5.4) increase post-ca. 1970 and peak in the early 1990s, followed by a subsequent decline. *Eunotia hemicyclus* (5.6) and *Aulacoseira distans* (6.3) both decline in relative abundance in the 1980s. Finally, *Frustulia pseudomagaliesmontana* (5.5) increases in relative abundance in the late 1990s. Diatom-inferred pH begins to decline in the 1950s and reaches its lowest values in the early 1990s.

Chrysophytes

Long-term (ca. 1780–2007) changes in chrysophyte abundances were similar to previously published work (Cumming et al. 1994; Majewski and Cumming 1999) (see Fig. 3). *Synura petersenii* (6.6) is present in the sedimentary profile from the early 1800s to the early 1900s and is subsequently rare or absent. *Synura echinulata* (6.0) and *Synura sphagnicola* (6.4) increase in relative abundance in the early 1900s, with *S. sphagnicola* decreasing after the mid-1950s. In contrast, *S. echinulata* experiences a second period of increase from

Fig. 4. Short-term (ca. 1965–2007) change in the relative abundance (%) of dominant (≥5%) diatom taxa in a ^{210}Pb-dated core from Big Moose Lake. Diatom species are arranged by pH-optimum given in the northeastern North America (NENA) dataset (Ginn et al. 2007*a*). Species not present in the NENA calibration set are demarked by NO (no optimum). Diatom-inferred pH (DI-pH) is based on a weighted-averaging model with a square-root species transformation (Ginn et al. 2007*a*). Period 1 (P1, ca. 1983–1993) and period 2 (P2, ca. 1997–2007) are shown.



the mid-1990s to ca. 2007. *Mallomonas hindonii* (4.8) is rare and intermittent in the sedimentary record prior to the mid-1970s, increases in relative abundance until the early 1990s, and then shows a subsequent decline. Likewise, *Mallomonas hamata* (5.6) increases in relative abundance in the early 1900s, from the 1970s to ca. 2000, and then shows a subsequent decline. *Mallomonas acaroides* (5.9) decreases in abundance from the early 1970s until it is rare or absent in the 1990s. Subsequently, the taxon shows a modest increase in abundance from ca. 2000–2007. Chrysophyte-inferred pH begins to decline in the early 1900s and reaches its lowest levels in the mid-1990s.

Cladocera

Long-term (ca. 1780–2007) and short-term (ca. 1965–2007) stratigraphies illustrate that the cladoceran assemblages of Big Moose Lake show little directional change prior to the late 1970s (see Figs. 3 and 6, respectively). The cladoceran species assemblages of Big Moose Lake are dominated by the planktonic genera *Bosmina* spp. and *Daphnia* spp., which combined make up between 69% and 91% of the total assemblage. In the late 1970s, the relative abundance of *Daphnia* and the littoral taxa decline, whereas *Bosmina* increases.

ANOSIM results: changes in species composition since ca. 1995

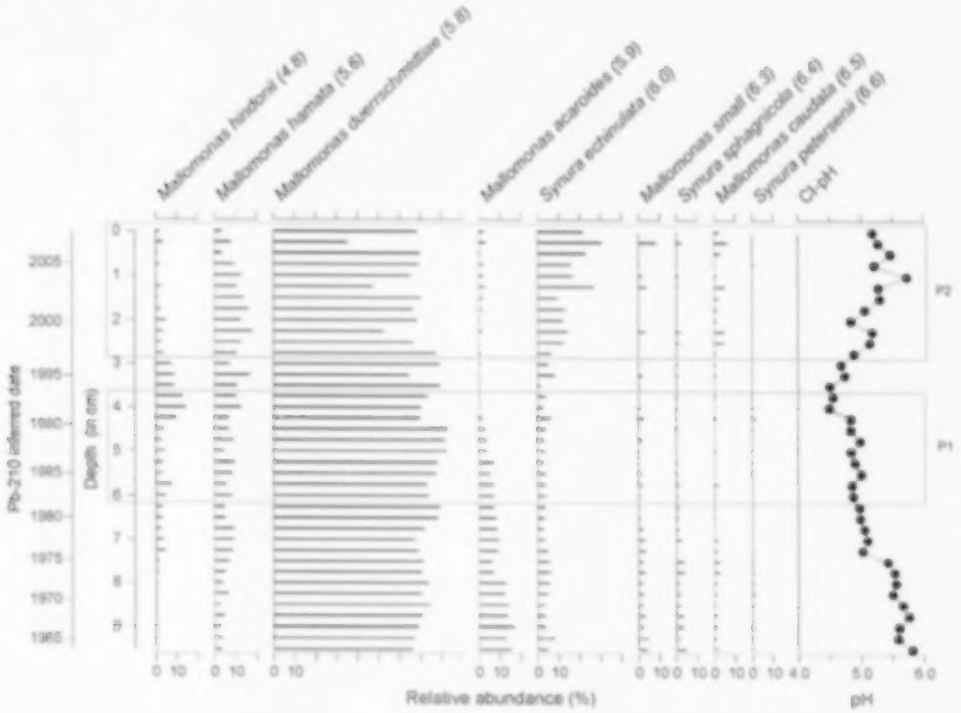
ANOSIM results show a significant shift in species composition between period 1 (ca. 1983–1993, mean pH = 5.14) and period 2 (ca. 1997–2007, mean pH = 5.54) for diatoms (n = 22, R = 0.15, p = 0.025) and chrysophytes (n = 22, R = 0.52, p = 0.001). The cladocera did not show a significant shift in species composition between period 1 and period 2 (n = 17, R = 0.08, p = 0.13). SIMPER post-hoc test identified eight diatom species and six chrysophyte species that contributed to more than 5% of the difference in species composition seen between period 1 and period 2, including several acid-tolerant taxa with low pH optima (see Table 1). Recent (post-ca. 1995) declines in chrysophyte and diatom taxa with low pH optima (i.e., *M. hindonii*, *M. hamata*, *F. acidobiontica*, *N. tenuicephala*), as well as increases in certain species with higher pH optima (i.e., *M. acaroides*, *M. caudata*, *F. pseudomagdaliesmontana*) appear to be consistent with biological recovery from acidification (see Figs. 4 and 5). However, although many taxa with low-pH optima show overall declines post-ca. 1995 (see Figs. 4 and 5), some have higher mean relative abundances in period 2 than period 1 (see Table 1).

RDA results: post-ca. 1995 species composition — chemical recovery vs. other factors

Diatoms

The correlations between the measured climatic and chemical variables used in the RDA of diatom and chrysophyte as-

Fig. 5. Short-term (ca. 1965–2007) change in the relative abundance (%) of dominant (≥5%) chrysophyte taxa in a ^{210}Pb-dated core from Big Moose Lake. Chrysophyte species are arranged by pH-optimum given in a 71-lake Adirondack calibration set (Cumming et al. 1992*a*). Chrysophyte-inferred pH (CI-pH) was inferred using a modern chrysophyte dataset of 71 Adirondack drainage lakes using a weighted-averaging model with tolerance down weighting and a ln + 1 transformation (Cumming et al. 1994). Period 1 (P1, ca. 1983–1993) and period 2 (P2, ca. 1997–2007) are shown.



semblage data show that with the exception of pH and Al, these variables are not highly correlated with each other (Table 2). Monte Carlo permutation tests found that only DOC showed a significant relationship with the diatom species data at $\alpha = 0.1$ (DOC, $p = 0.062$). The first ordination axis of the RDA explains approximately 8% of the species-environmental variation in the short-term (ca. 1983–2007) diatom assemblages of Big Moose Lake when constrained with DOC (see Fig. 7*a*). The RDA shows some separation between the diatom assemblages between period 1 (ca. 1983 to 1993) and period 2 (ca. 1997 to 2007). The assemblages of period 1 are characterized by higher levels of *F. acidobiontica* and are associated with lower DOC concentrations (see Fig. 7*a*). Conversely, the diatom assemblages of period 2 are characterized by lower levels of *F. acidobiontica* and higher levels of *F. pseudomagaliesmontana*, *Frustulia constricta*, and *Frustulia rhomboides* var. *saxonica*, and are associated with higher DOC concentrations (see Fig. 7*a*). Though pH was not found to be significant and was only plotted passively in the ordination, it appears that the species assemblages of period 2 are generally associated with higher pH levels than the period 1 assemblages.

Chrysophytes

Monte Carlo permutation tests found that pH, DOC, and total annual precipitation (A_{prep}) showed a significant relationship with the species data at $\alpha = 0.1$ (pH, $p = 0.002$; DOC, $p = 0.089$; A_{prep}, $p = 0.098$). The first two ordination axes of the RDA explain approximately 48% of the species-environmental variation in the short-term (ca. 1983–2007) chrysophyte assemblages of Big Moose Lake when constrained to pH, DOC, and A_{prep} (see Fig. 7*b*). The RDA reveals a separation between species assemblages of period 1 (ca. 1983–1993) and period 2 (ca. 1997–2007) (see Fig. 7*b*). The species assemblages of period 1 are characterized by higher levels of *Mallomonas duerrschmidtiae*, *M. acaroides*, and *M. hindonii*, and are associated with lower pH and DOC levels. Additionally, certain intervals from the early 1990s appear to be associated with higher total annual precipitation (see Fig. 7*b*). The species assemblages of period 2 are characterized by lower levels of *M. hindonii* as well as higher levels of *S. echinulata* and *M. caudata* (see Fig. 7*b*). Period 2 assemblages are associated with higher pH (see Fig. 7*b*). Additionally, most of the post-ca. 2000 species assemblages are associated with higher DOC concentrations.

PCA results: a comparison with pre-disturbance conditions

Diatoms

The first two ordination axes of the PCA ordination diagram account for approximately 64% of the variation in the

Fig. 6. Short-term (ca. 1965–2007) change in the relative abundance (%) of dominant (≥5%) cladoceran taxa in a ^{210}Pb-dated core from Big Moose Lake. Chrysophyte-inferred pH (CI-pH) was inferred using a modern chrysophyte dataset of 71 Adirondack drainage lakes using a weighted-averaging model with tolerance down weighting and a ln + 1 transformation (Cumming et al. 1994). Diatom-inferred pH (DI-pH) is based on a weighted-averaging model with a square-root species transformation (Ginn et al. 2007*a*). Period 1 (P1, ca. 1983–1993) and period 2 (P2, ca. 1997–2007) are shown.

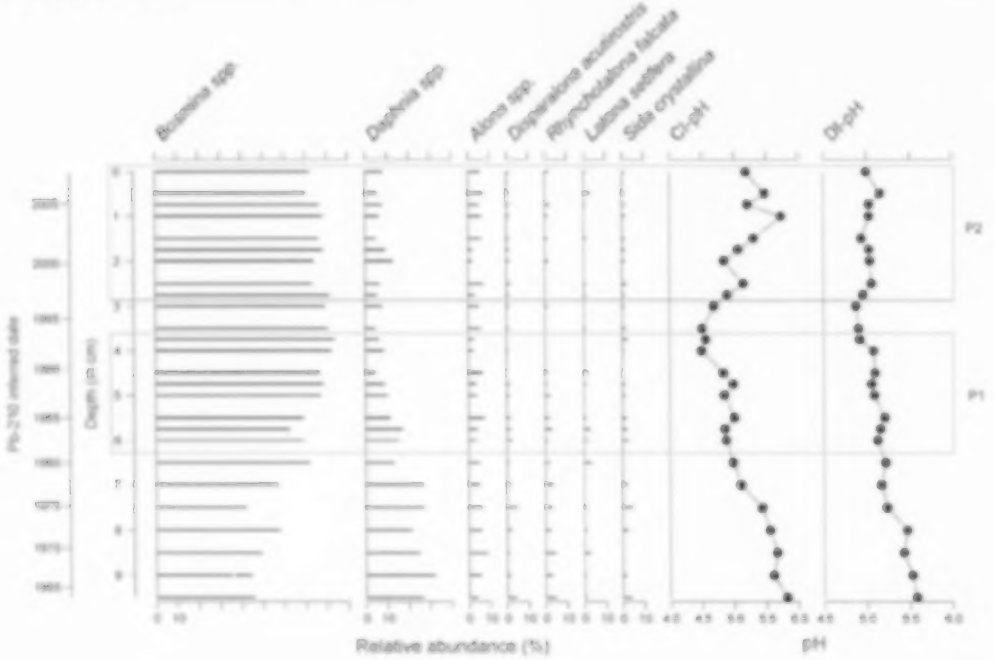


Table 1. Similarities percentage test (SIMPER) results for differences in diatom and chrysophyte species composition between period 1 (ca. 1983–1993) and period 2 (ca. 1997–2007).

Species	Mean RA in period 1	Mean RA in period 2	Contribution (%)
Chrysophytes			
Mallomonas duerrschmidtiae (5.8)	76.2	63.0	31.3
Synura echinulata (6.0)	3.4	16.7	30.3
Mallomonas hamata (5.6)	8.1	10.8	10.7
Mallomonas hindonii (4.8)	6.4	2.2	10.1
Mallomonas acaroides (5.9)	3.8	1.5	6.7
Mallomonas caudata (6.5)	0.5	2.7	5.2
Diatoms			
Navicula tenuicephala (5.4)	8.7	9.5	11.5
Fragilaria acidobiontica (5.1)	11.4	11.6	8.8
Eunotia curvata (5.9)	3.9	4.3	8.0
Frustulia pseudomagaliesmontana (5.5)	2.3	4.4	7.3
Frustulia rhomboides (6.0)	1.8	1.5	5.8
Frustulia rhomboides var. saxonica (5.9)	1.5	2.9	5.6
Aulacoseira nygaardii (6.4)	3.0	1.4	5.4
Tabellaria quadrisepta (5.4)	7.4	6.7	5.3

Note: Mean species relative abundance (RA) in periods 1 and 2 are given, as well as the percent contribution (Contribution (%)) each species made to the overall dissimilarity between time periods. Species pH optima as listed in Cumming et al. 1992*a* (chrysophytes) and Ginn et al. 2007*a* (diatoms) are provided in brackets after species name.

Table 2. Correlations of environmental variables used in a Redundancy Analysis of sedimentary diatom and chrysophytes assemblages from ca. 1983–2007.

	DOC	Si	Al	pH	T_{snow}	T_{prep}	T_{temp}
DOC	1	—	—	—	—	—	—
Si	–0.17	1	—	—	—	—	—
Al	–0.13	–0.03	1	—	—	—	—
pH	0.34	0.12	**–0.63**	1	—	—	—
T_{snow}	–0.34	0.10	–0.16	0.35	1	—	—
A_{prep}	0.22	–0.15	0.38	–0.30	–0.33	1	—
A_{temp}	0.30	–0.32	–0.31	0.26	–0.35	–0.11	1

Note: Measured chemical variables are reported as yearly averages. Four chemical variables are shown: dissolved organic carbon (DOC, μmol C·L^{-1}), SiO_2 (Si, μmol·L^{-1}), total monomeric aluminum (Al, μmol·L^{-1}) and pH. Total annual snowfall (T_{snow}, cm) is based on uncorrected snowfall data. Total annual precipitation (A_{prep}, cm) and average annual temperature (A_{temp}, °C) are based on quality-assured climatic data. Environmental variables that are significantly correlated ($p < 0.05$) are in bold font.

long-term (ca. 1780–2007) diatom assemblages of Big Moose Lake (see Fig. 8*a*). *Tabellaria flocculosa* strain IIIp, *N. tenuicephala*, and *F. acidobiontica* are strongly correlated with PCA axis-1, whereas *Eunotia bilunaris* var. *mucophilia* and *Eunotia curvata* are strongly correlated with PCA axis-2. The pre-disturbance (pre. ca. 1900) diatom assemblages are characterized by circumneutral taxa (i.e., *C. stelligera*, *T. flocculosa*, strain IIIp, etc.) (see Figs. 3 and 8*a*). The early disturbance assemblages (post-ca. 1900 – ca.1950) are similar in species composition to the pre-disturbance community. The post-1950 community is also similar in species composition until the mid-1970s, where the assemblages become characterized by increasing levels of *N. tenuicephala* and *F. acidobiontica*. The diatoms show little directional change in composition since the 1995 implementation of the ARP and remain characterized by acid-tolerant taxa. As such, it is apparent that the diatom taxa of Big Moose Lake have not returned to a pre-disturbance (pre-ca. 1900) ecological condition since the implementation of the ARP (see Fig. 8*a*).

Chrysophytes

The first two axes of the PCA ordination diagram explained approximately 84% of the variation in the long-term (ca. 1780–2007) chrysophyte assemblages of Big Moose Lake (see Fig. 8*b*). *Mallomonas duerrschmidtiae* and *S. echinulata* are strongly correlated with PCA axis-1, whereas *M. hindonii* and *S. sphagnicola* are strongly correlated with PCA axis-2. The pre-disturbance (pre-ca. 1900) species assemblage of Big Moose Lake is characterized by high levels of *M. duerrschmidtiae*, *M. acaroides*, and *S. petersenii* (see Figs. 3 and 8*b*). The early disturbance assemblage (ca. 1900 – ca. pre-1950) is similar in species composition to the pre-disturbance community, though some intervals are characterized by higher levels of *S. sphagnicola*. The post-1950 assemblage shows little change in ordination space until the mid-1970s, where *M. hindonii* increases. The post-ca. 1995 (post-ARP) assemblage is characterized by lower levels of *M. hindonii*, and higher levels of *M. caudata* and *S. echinulata*. Based on this current species composition, it is apparent that the chrysophyte assemblages of Big Moose Lake are not returning to a pre-disturbance (pre-ca. 1900) ecological condition (see Fig. 8*b*).

Discussion

The results of this study clearly demonstrate a differential response between algal and zooplankton groups. Although both diatoms and chrysophytes were found to show a significant shift in species composition after the 1995 implementation of the ARP, the changes in the diatom community were modest. In contrast, the cladocera show no response to chemical recovery in Big Moose Lake as of yet. In the following sections we discuss the apparent differences between species groups in greater detail.

Community response to chemical recovery: diatoms and chrysophytes

Results of the ANOSIM and SIMPER tests suggest that biological recovery from acidification is occurring, or beginning to occur, in the diatom and chrysophyte species communities of Big Moose Lake. Recent (post-ca. 1995) declines in chrysophyte and diatom taxa with low-pH optima (i.e., *M. hindonii*, *M. hamata*, *F. acidobiontica*, *N. tenuicephala*) as well as increases in certain species with higher-pH optima (i.e., *M. acaroides*, *M. caudata*, and *F. pseudomagaliesmontana*) appear to be consistent with biological recovery from acidification. ANOSIM identified a significant shift in species composition in both algal groups after the 1995 implementation of the ARP and SIMPER found that the species that contributed to the post-ca. 1995 changes in species composition included several chrysophyte/diatom taxa with low-pH optima. Additionally, the RDA revealed that post-ca. 1995 declines in acid-tolerant taxa such as *F. acidobiontica* (pH optimum 5.1) and *M. hindonii* (pH optimum 4.8) appear to be associated with increases in pH.

Although both species groups appear to be responding to chemical recovery in Big Moose Lake, the magnitude of their responses differ. ANOSIM revealed that the separation between the diatom assemblages in period 1 (ca. 1983–1993) and period 2 (ca. 1997–2007) was modest compared with the chrysophytes ($R = 0.15$, diatoms; $R = 0.52$, chrysophytes). Likewise, although both the post-ca. 1995 diatom and chrysophyte assemblages of Big Moose Lake are associated with higher pH levels, the relationship is only significant for the chrysophytes ($p = 0.002$, chrysophytes; $p = 0.22$, diatoms). The differential response of diatoms and chrysophytes to increases in lake-water pH may be at least partially related to the life history strategies of the two algal groups. Previous investigations have suggested that chrysophytes are more sensitive to changes in pH than diatoms, because chrysophytes are exclusively planktonic (Charles and Smol 1988; Cumming et al. 1992*b*). Additionally, many chrysophyte species such as *M. hindonii* are abundant during the winter and

Fig. 7. Redundancy analysis (RDA) of sedimentary diatom (A) and chrysophyte (B) assemblages from ca. 1983–2007 in Big Moose Lake. Environmental variables significant at $p = 0.1$ are shown as thick black arrows and nonsignificant environmental variables are plotted passively as thick grey arrows. Species are shown as thin black arrows and sediment intervals are shown as points. Years are based on ^{210}Pb-inferred year. Samples belonging to period 1 (ca. 1983–1993) are shown as white circles (○), samples belonging to period 2 (ca. 1997–2007) are shown as black circles (●), and samples belonging to neither period 1 nor period 2 are shown as grey triangles (△). Environmental variables are pH, total monomeric aluminum (Al, μmol·L^{-1}), dissolved organic carbon (DOC, μmol C·L^{-1}), SiO_2 (Si, μmol·L^{-1}), average annual temperature (T_{temp}, °C), total annual precipitation (T_{prep}, cm), and total monthly snowfall (T_{snow}, cm). First and second Eigenvalues (λ_1 and λ_2, respectively) are given for each RDA. Note that λ_2 in the diatom RDA (A) is an unconstrained Eigenvalue. Species codes are based on the NENA (diatoms) and PIRLA (chrysophyte) calibration sets. Diatoms: *Achnanthes altaica* (ACaltc), *Astrionella ralfsii* var. *americana* (ASra.a.l), *Aulacoseira distans* (AUdstns), *Aulacoseira nygaardii* (AUnygaar), *Anomoeoneis brebissonii* (BRbrbssn), *Cyclotella stelligera* (CYstllga) *Eunotia bilunaris* var. *mucophilia* (EUbil.mu), *Eunotia carolina* (EUcrln), *Eunotia curvata* (EUcrvt), *Eunotia incisa* (EUincisa), *Eunotia nymanniana* (EU.nym), *Fragilaria acidobiontica* (FFacidob), *Fragilaria constricta* (FFcnstrc), *Frustulia pseudomagaliesmontana* (FSpsdmgl), *Frustulia rhomboides* var. *saxonica* (FSsxnc), *Frustulia rhomboides* (FSrhmbds), *Navicula tenuicephala* (NAtncphl), *Eunotia hemicyclus* (SOhmccls), *Tabellaria flocculosa* strain IIIp (TAfloc.3p), *Tabellaria flocculosa* strain IV (TAfloc.4), *Tabellaria quadrisepta* (TAqdrspt). Chrysophytes: *Mallomonas acaroides* (M acar), *Mallomonas caudata* (M caud), *Mallomonas duerrschmidtiae* (M duerrs), *Mallomonas hindonii* (M hind), *Mallomonas hamata* (M hamata), *Mallomonas small* (M small), *Synura echinulata* (Sy echin), *Synura petersenii* (Sy peter), *Synura sphagnicola* (Sy sphag).

spring months, the period of lowest seasonal pH levels (Siver 1991). Thus, the taxa may be more responsive to modest increases in spring pH, such as those documented in Big Moose Lake.

PCA revealed that neither the diatoms nor the chrysophytes are moving towards their pre-disturbance ecological assemblage. In the case of the diatoms, it appears that there has been little directional change in the species assemblages since the 1995 implementation of the ARP. In contrast, the chrysophyte assemblages appear to be moving towards a new ecological condition, driven in part by recent (post-ca. 1995) increases in the unicellular chrysophyte taxon *M. caudata* and the colonial chrysophyte taxon *S. echinulata*.

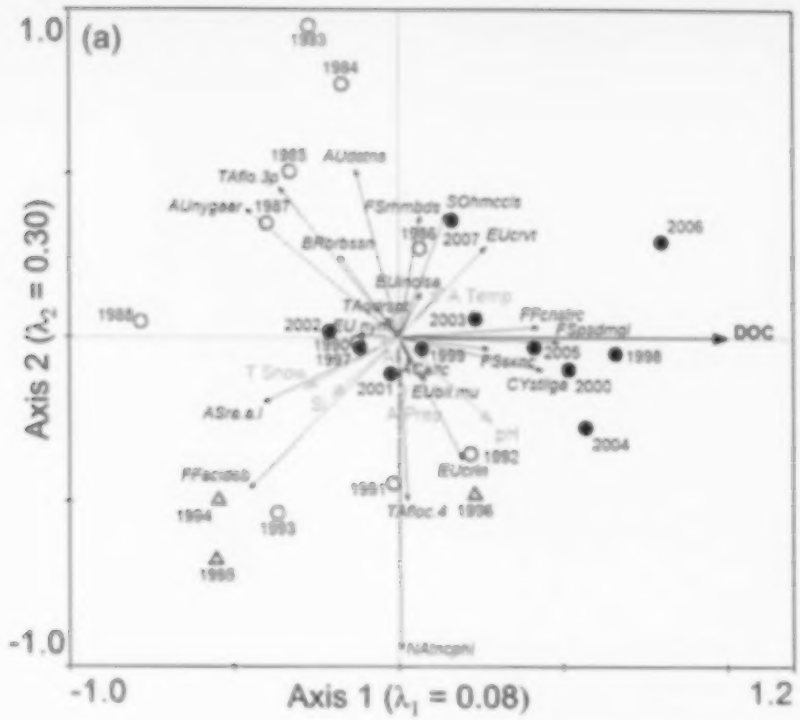
Mallomonas caudata has a pH optimum of 6.5, and so can be classified as a "pH sensitive" chrysophyte species. Thus, post-ca. 1995 increases in its abundance may be at least partially related to recent increases in lake-water pH in Big Moose Lake. However, RDA revealed that the increase in *M. caudata* is also correlated with increases in DOC concentrations. Likewise, the post-ca. 1995 increase in the diatom *F. pseudomagaliesmontana* (pH optimum 5.5) is correlated with increases in DOC. Previous investigations have associated both *M. caudata* (Ginn et al. 2010) and *F. pseudomagaliesmontana* (Ginn et al. 2007*a*) with elevated lake-DOC concentrations. DOC concentrations in Big Moose Lake have been increasing since the mid-1990s (Driscoll et al. 2003), a trend that was observed in 15 of 48 long-term monitoring sites in the Adirondacks from 1992–2004 (Driscoll et al. 2007). Similar trends in DOC have been reported in a variety of acid-impacted locations worldwide (Monteith et al. 2007). Regional controls on DOC are complex, and have been related to declines in sulphate deposition (Evans et al. 2006; Monteith et al. 2007) as well as changes in local environmental conditions (e.g., temperature (Keller et al. 2008), precipitation, and total solar radiation, Zhang et al. 2010). As such, recent (post-1995) increases in *M. caudata* and *F. pseudomagaliesmontana* may be potentially related to chemical recovery from acid deposition and (or) changes in local climate in the Adirondack region.

Synura echinulata, a colonial chrysophyte, has reached historic highs in the recent (post-ca. 1995) sedimentary assemblages of Big Moose Lake. Similar increases in the relative abundance of colonial chrysophytes have been documented in boreal lakes in Ontario (Paterson et al. 2004, 2008; Hyatt et al. 2010). In the aforementioned studies, the increases in colonial chrysophytes were attributed, at least in part, to recent climate warming. It has been suggested that a warming-induced shortening of the ice-covered season may lead to alterations in lake thermal structure that would be beneficial to colonial chrysophytes (Paterson et al. 2004; Hyatt et al. 2010). A shortening of the ice-covered season often causes an earlier onset of thermal stratification and an increase in the length of the stratification period (Keller 2007; Vincent 2009). Colonial chrysophytes may therefore have a competitive advantage with prolonged stratification as they can regulate their positions in the water-column to benefit from optimal light/nutrient environments (Findlay et al. 2001).

Although average annual temperature was not found to be significant in the chrysophyte RDA, this may have been due to the short sampling time period (ca. 1983–2007). In contrast, a recent analysis of weather data in the Adirondack Park suggested that mean annual *air* temperature has increased in concordance with increases global average temperature from 1975 to 2005, although between-year variability is high (Stager et al. 2009). Additionally, several Adirondack lakes have experienced a shortening of their ice-covered seasons, owing to later ice-on and (or) earlier ice-off dates (Magnuson et al. 2000; Stager et al. 2009). These trends are consistent with other regions that have linked increases in air temperature to a shortening of ice-covered season in both lakes and rivers (Magnuson et al. 2000; Duguay et al. 2006). Thus, recent alterations in lake thermal structure may provide a plausible mechanism for the increased abundance of colonial chrysophytes in Big Moose Lake and, by extension, the inability of the chrysophyte community to return to its pre-acidification assemblage.

Community response to chemical recovery: cladocera

The decline in the relative abundance of *Daphnia* in Big Moose Lake was likely due to acidification and (or) low calcium concentrations in the late 1970s. Both DI and Cl-pH were near or below 5.0 in the late 1970s, a result that is consistent with other inferred pH values for Big Moose Lake


(a)
1.0
-1.0
-1.0
1.2
Axis 2 (λ_2 = 0.30)
Axis 1 (λ_1 = 0.08)
DOC
A Temp
T Snow
pH
Al
1983
1984
1985
1986
1987
2006
1988
2002
2003
1999
1998
2005
2001
2000
2004
1992
1991
1994
1993
1995
AUtetra
TAflo.3p
AUnygaer
FSmmbds
SOhmccls
2007
EUcrvt
BRorbsan
BUnolsa
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EUcrin
TAfloc.4
*NAhcgnl

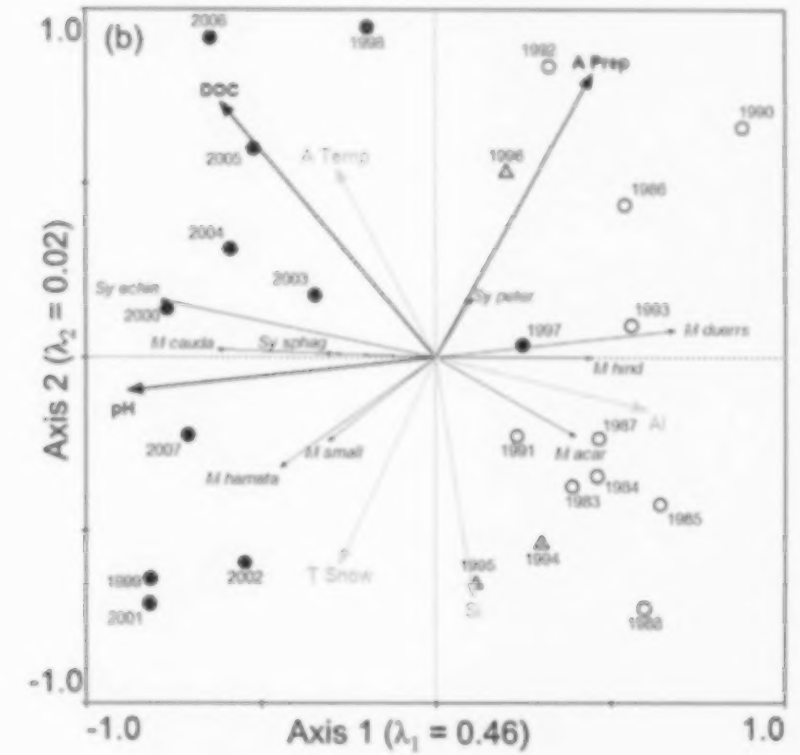
(b)
1.0
-1.0
-1.0
1.0
Axis 2 (λ_2 = 0.02)
Axis 1 (λ_1 = 0.46)
DOC
A Prep
A Temp
pH
Al
T Snow
2006
1998
1992
1990
2005
1996
1986
2004
2003
Sy echin
Sy pellor
2000
1993
1997
M duerrs
M caudis
Sy sphag
M hind
2007
M small
1991
M acar
M hamata
1987
1984
1983
1985
1994
2002
1999
1995
2001
1988

Fig. 8. Principal Components Analysis of sedimentary diatom (A) and chrysophyte (B) assemblages from ca. 1780–2007 in Big Moose Lake. Species are shown as arrows and sediment intervals are points. Four a priori defined time periods are differentiated by symbols: pre-ca. 1900 (pre-disturbance, white square (□)), ca. 1900 – pre-ca.1950 (early disturbance, white triangle (△)), ca. 1950 – ca. 1995 (acidification, grey diamond ◇), and post-ca. 1995 – 2007 (post-ARP, black circle ●). Species codes are based on the NENA (diatoms) and PIRLA (chrysophyte) calibration sets. Diatoms: *Achnanthes altaica* (ACaltc), *Astrionella ralfsii* var. *americana* (ASra.a.l), *Aulacoseira distans* (AUdstns), *Aulacoseira nygaardii* (AUnygaar), *Anomoeoneis brebissonii* (BRbrbssn), *Cyclotella stelligera* (CYstllga) *Eunotia bilunaris* var. *mucophilia* (EUbil.mu), *Eunotia carolina* (EUcrln), *Eunotia curvata* (EUcrvt), *Eunotia incisa* (EUincisa), *Eunotia nymanniana* (EU.nym), *Fragilaria acidobiontica* (FFacidob), *Fragilaria constricta* (FFcnstrc), *Fragilaria pseudoinaguliesmontana* (FSpsdmgl), *Frustulia rhomboides* var. *saxonica* (FSsxnc), *Frustulia rhomboides* (FSrhmbds), *Navicula tenuicephala* (NAtncphl), *Eunotia hemicyclus* (SObmccls), *Tabellaria flocculosa* strain *IIIp* (TAfloc.3p), *Tabellaria flocculosa* strain *IV* (TAfloc.4), *Tabellaria quadrisepta* (TAqdrspt). Chrysophytes: *Mallomonas acaroides* (M acar), *Mallomonas caudata* (M caud), *Mallomonas duerrschmidtiae* (M duerrs), *Mallomonas hindonii* (M hind), *Mallomonas hamata* (M hamata), *Mallomonas small* (M small), *Synura echinulata* (Sy echin), *Synura petersenii* (Sy peter), *Synura sphagnicola* (Sy sphag).

(e.g., Charles et al. 1990; Cumming et al. 1994; Majewski and Cumming 1999). Most daphniids are acid-sensitive organisms, and their relative abundance in a waterbody tends to decline with acidification (Marmorek and Korman 1993; Gray and Arnott 2009). *Bosmina*, in turn, tends to increase in relative abundance as daphniids decline, possibly owing to a release from competition in the pelagic zone (Locke and Sprules 2000). Additionally, calcium concentrations were likely relatively low in Big Moose Lake in the late 1970s (i.e., average Ca^{2+} concentration in 1983, 1.95 mg·L^{-1}). Previous research has demonstrated that calcium-sensitive daphniids such as *D. pulex* (a member of the *D.* cf. *pulex* complex) can decline in abundance in a waterbody with dissolved calcium less than 2.0 mg·L^{-1} (Jeziorski et al. 2008), possibly owing to a reduced rate of reproduction (Ashforth and Yan 2008).

Calcium concentrations in Big Moose Lake may prove to be limiting to some calcium-sensitive daphniids as chemical recovery from acidification progresses. Long-term sampling of zooplankton in Big Moose Lake from 1994 to 2006, carried out as part of the Adirondack Acidification Effects Program, found that the species assemblage in Big Moose Lake is dominated by *Daphnia catawba*, with *D. pulex* forming small ephemeral populations (W. Shaw, Visiting Scientist at the Darrin Freshwater Institute, Rensselaer Polytechnic Institute, New York, USA, personal communication 2010). As stated previously, *D. pulex* is a calcium-sensitive daphniid, and so its presence in Big Moose Lake may be limited by the lake's present low-calcium concentrations (i.e., <2.0 mg·L^{-1}) (Jeziorski et al. 2008). However, modelling studies on Adirondack lakes have suggested that present-day calcium concentrations are higher than those of pre-industrial times (~1850, Zhai et al. 2008). As such, more research into the possible role watershed calcium-depletion may play in limiting cladoceran biological recovery from acidification in Adirondack lakes is required.

Biological factors may have also contributed to the lack of recovery seen in the cladoceran taxa. Lake trout were extirpated from Big Moose Lake in the mid-1960s (Schofield and Driscoll 1987). The extirpation of a dominant piscivore can result in increased planktivory on large zooplankton taxa such as daphniids (Leavitt et al. 1989). Previous investigations have shown that increased predation alone may prevent biological recovery from acidification in zooplankton groups, even in cases where liming has occurred (e.g., Nilssen and Wævågen 2002). Thus, cladoceran recovery may be limited until the return of a pre-disturbance fish assemblage to Big Moose Lake.

Big Moose Lake in the big picture: potential for recovery in the Adirondacks

This study provides evidence of biological recovery from acidification in an acid-impacted Adirondack lake. The recent shifts in species composition in Big Moose Lake between 1995 and 2007 are modest. Though some changes in chrysophyte and diatom species composition were noted that are consistent with biological recovery from acidification (i.e., a decrease in taxa with low pH optima, and an increase in taxa with a higher pH optima), the communities have not shown movement towards their pre-disturbance assemblages. Additionally, recent (post-ca. 1995) changes in certain taxa (e.g., *S. echinulata*) may be related to an effect of climate warming. As such, it appears unlikely that acid-impacted algal assemblages will return to their pre-disturbance state. Cladoceran taxa were not found to show a change in community composition with increases in pH, possibly owing to low lake-water calcium concentrations and (or) altered predation regimes.

It is important to understand that the onset of biological recovery from acidification is determined by both site-specific and regional environmental conditions. As such, the trends in Big Moose Lake should not be taken as representative of the Adirondack region as a whole. However, this detailed paleolimnological case study highlights certain recovery trends that may be investigated in further, regional surveys of Adirondack lakes recovering from acid deposition. Modelling studies have suggested that many Adirondack lakes will still have pH values below 6.0 and ANC values below 50 μeq·L^{-1} by 2050 (Chen and Driscoll 2005). Biological recovery will therefore likely be a protracted process during which species assemblages are likely to be influenced by other environmental stressors, including a changing climate.

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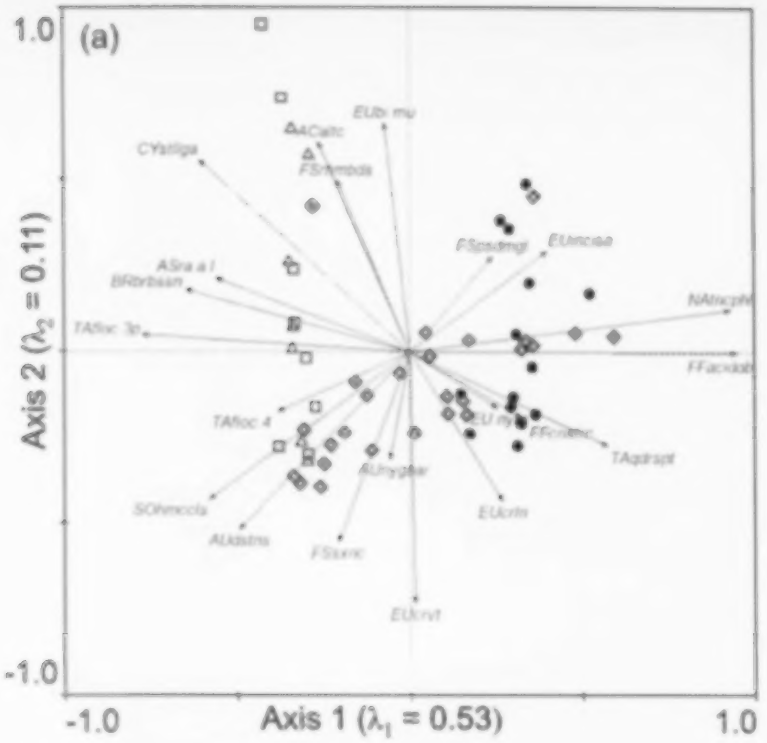
(a)
1.0
-1.0
-1.0
1.0
Axis 2 (λ_2 = 0.11)
Axis 1 (λ_1 = 0.53)
EUbi mu
ACalic
CYstiga
FShimbda
FSpsdmgl
EUmcrae
ASra a l
BRorbsan
NAtrcph
TAfloc 3p
FFacksbt
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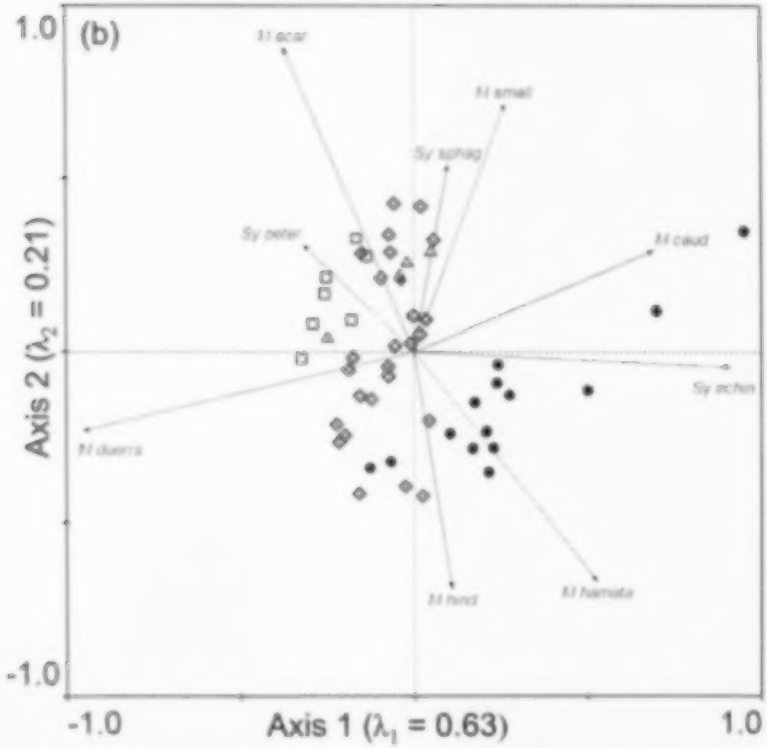
(b)
1.0
-1.0
-1.0
1.0
Axis 2 (λ_2 = 0.21)
Axis 1 (λ_1 = 0.63)
M acar
M smal
Sy sphag
Sy peter
M caud
Sy echin
M diverra
M hord
M hamata

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Appendix A

Table A1. Means and medians of monthly chemical/climatic variables for Big Moose Lake in two a priori defined time periods (period 1, 1983–1993; period 2, 1997–2007).

	N		Mean		Median			
Variable	P1	P2	P1	P2	P1	P2	*U*	*p*
$SO_4^{2-} + NO_3^-$	129	132	154.77	106.62	152.80	103.90	16518.5	<0.0001
pH	129	132	5.14	5.54	5.13	5.54	2632.5	<0.0001
ANC	129	132	–0.42	12.99	0.70	13.01	1740.0	<0.0001
Al	128	132	6.48	4.97	5.86	4.19	10885.0	<0.0001
Ca	128	132	1.91	1.53	1.89	1.50	16252.5	<0.0001
DOC	128	132	321.01	375.83	308.06	368.45	4935.5	<0.0001
SiO_2	128	132	70.86	71.95	66.36	68.65	8132.5	0.603
T_{avg}	132	132	5.74	6.28	6.42	6.61	8410.0	0.626
T_{precip}	132	132	9.19	8.61	8.54	7.97	9621.5	0.143
T_{snow}	132	132	30.65	34.86	2.00	3.00	8357.5	0.544

Note: Environmental variables are sulphate and nitrate ($SO_4^{2-} + NO_3^-$, $\mu eq \cdot L^{-1}$), pH, acid neutralizing capacity (ANC, $\mu eq \cdot L^{-1}$), total monomeric aluminum (Al, $\mu mol \cdot L^{-1}$), calcium (Ca, $mg \cdot L^{-1}$), dissolved organic carbon (DOC, $\mu mol\ C \cdot L^{-1}$), SiO_2 ($\mu mol \cdot L^{-1}$), average monthly temperature (T_{avg}, °C), total monthly precipitation (T_{precip}, cm), and total monthly snowfall (T_{snow}, cm). A Mann–Whitney *U* test was applied to identify whether there was a significant ($p = 0.05$) difference between the medians of chemical/climatic variables measured between period 1 (P1) and period 2 (P2). The number of samples (*N*), the mean, and the median of each environmental variable are given for each time period. The Mann–Whitney *U* test statistic (*U*) and the *p* value (*p*) are given. The *p* values are significant at $\alpha \leq 0.05$.

Maintenance of asymmetric hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) via postzygotic barriers and paternal effects

David Álvarez and Eva Garcia-Vazquez

Abstract: At the southern European edge of Atlantic salmon (*Salmo salar*) distribution, all the hybrids found in nature are the product of crosses between female salmon and male brown trout (*Salmo trutta*). By artificially producing reciprocal crosses between salmon and trout, we demonstrate that unidirectional hybridization observed in nature is the result of postzygotic barriers that produce very high mortality rates (95%) in female trout × male salmon hybrids and not the consequence of prezygotic isolation or behavioural differences between the two species. Mortality of female trout × male salmon hybrids mainly occurs during the last phases of development, and a high percentage of these surviving hybrids showed external deformities that could compromise survival in the wild. Another important finding is the existence of paternal factor in embryo development. Using time to midhatch as an indicator of developmental rate, female salmon × male trout hybrids hatched faster than female trout × male salmon hybrids, with both developing at a rate intermediate to the pure crosses. The early emergence of female salmon × male trout hybrids, which have similar survival to pure salmons, could have fitness repercussions, since early emerging fry have a competitive advantage over later emerging fry.

Résumé : À la marge sud de la répartition européenne du saumon atlantique (*Salmo salar*), tous les hybrides retrouvés en nature proviennent de croisements entre des saumons femelles et des truites brunes (*Salmo trutta*) mâles. En produisant artificiellement des croisements réciproques entre le saumon et la truite, nous démontrons que l'hybridation unidirectionnelle observée en nature est le résultat de barrières postzygotiques qui produisent de très forts taux de mortalité (95 %) chez les hybrides de truite femelle × saumon mâle et non la conséquence d'isolement prézygotique, ni de différences de comportement entre les deux espèces. La mortalité des hybrides de truite femelle × saumon mâle se produit surtout durant les phases finales du développement et un fort pourcentage des hybrides survivants présentent des malformations externes qui pourraient compromettre leur survie en nature. Une autre découverte importante est l'existence d'un facteur paternel dans le développement embryonnaire. D'après le temps requis pour atteindre le milieu de l'éclosion utilisé comme indication du taux de développement, les hybrides de saumon femelle × truite mâle éclosent plus rapidement que les hybrides truite femelle × saumon mâle, les deux se développant à un taux intermédiaire entre ceux des croisements purs. L'émergence hâtive des hybrides de saumon femelle × truite mâle, qui ont une survie semblable à celle des saumons purs, pourrait avoir des répercussions sur la fitness, puisque les alevins qui émergent tôt ont un avantage compétitif sur ceux qui émergent plus tard.

[Traduit par la Rédaction]

Introduction

The nature of reproductive isolation among closely related species is a central point in evolutionary biology (Coyne and Orr 2004). Species are genetically distinct, but interspecific hybridization between close, related species occurs frequently in the wild (Mallet 2005). A major consequence of such hybridization may be the outbreeding depression due to the loss of unique genetic complexes and disruption of local adaptations (Barton and Hewitt 1985).

Hybridization is more common in fishes than in other vertebrate taxa (Leary et al. 1995). Among the Salmonidae family, hybridization has been recorded in almost all the genera (*Salmo*, *Salvelinus*, *Coregonus*, and *Oncorhynchus*), but it does appear that hybridization is much less common within the Pacific coast genus *Oncorhynchus* than within other salmonids (Taylor 2004). These differences in the incidence of hybridization among Salmonidae could be explained because hybridization and introgression were much more common in freshwater resident populations within both genera than in anadromous populations (Taylor 2004). In many cases, hybridization and introgression in this family has been mediated by human introductions and restocking practises (Allendorf et al. 2001), and in a broad sense, hybridization usually occurs in areas where one of the two species involved no longer exist (Taylor 2004). For example, four species of *Oncorhynchus*

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have been introduced into the Great Lakes region of North America during the last century, and currently introgressive hybridization has been detected between pink salmon (*Oncorhynchus gorbuscha*) and Chinook salmon (*Oncorhynchus tshawytscha*), although hybrids between these two species have never been detected in their natural distribution range (Rosenfield et al. 2000). For instance, in Newfoundland waters, hybridization between non-native brown trout (*Salmo trutta*) and native Atlantic salmon (*Salmo salar*) occurred at a rate twice that reported in European rivers, where both species are native (McGowan and Davidson 1992).

In undisturbed ecosystems, natural hybridization is hindered by biological barriers that can be classified into two major groups depending on whether gene exchange is blocked before (prezygotic isolation) or after (postzygotic isolation) mating (Wu and Palopoli 1994; Servedio and Noor 2003).

Prezygotic isolation usually occurs through behavioural differences between the two species, for example, differences in breeding time or location or in the process of mate choice. When these barriers are broken or absent, there are mechanisms that hinder the combination of gametes of different species. Recent studies of competitive mating in marine invertebrates have demonstrated that eggs can show a marked preference for conspecifics when offered a mix from homo- and hetero-specific sperm (Geyer and Palumbi 2005). Heterospecific sperm is usually rejected by the egg (O'Rand 1988), but in some cases can avoid this selective filter and fertilize the ovum.

After fertilization, there are mechanisms that can lead to the abortion of hybrid embryos. These include genetic incompatibilities, polyploidization, chromosomal rearrangements, and cytoplasmic incompatibilities (Coyne and Orr 2004). These mechanisms are some of the postmating barriers that reduce the probability of interspecific fertilization.

There are two possibilities for the origin of the hybrids: (*i*) hybrids arise by matings of females of species A with males of species B and vice versa (reciprocal hybridization), or (*ii*) hybrids arise by matings of females of species A with males of species B, but not reciprocally (unidirectional or asymmetric hybridization). Asymmetric hybridization is a widespread phenomenon across a wide range of taxa (Turelli and Moyle 2007). In fishes, asymmetric hybridization has been documented in many species of salmonids and other fish families (see references in Wirtz 1999), for example, mitochondrial DNA analyses have revealed that hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) is usually asymmetric but which of those species is the maternal species varies among populations. While in North America the maternal species is brown trout (McGowan and Davidson 1992; Gephard et al. 2000), in the south of Europe the maternal species is usually the Atlantic salmon (Garcia-Vazquez et al. 2002). In other European areas, the maternal component can come either from brown trout or from Atlantic salmon (Youngson et al. 1993; Hartley 1996; Jansson and Öst 1997). The direction of the cross could be explained by differences in relative density between the two species (Crozier 1984; Pyle and Randall 1994) or by genetic incompatibilities between gametes that can favour one direction of the cross and hinder the other one (Baird et al. 1992; Wu and Palopoli 1994).

Atlantic salmon and brown trout are sympatric in most of their geographical range and in natural populations without human manipulation; the percentage of interspecific hybrids between them rarely exceeds 1% of the total population (Hurrell and Price 1991), which implies that there normally exist efficient mechanisms of reproductive isolation between the two species. However, hybridization between both species can sometimes be much higher (e.g., up to 18% of all genotypes present in some Scottish lakes are hybrids; Hartley 1996) because of various causes (Vuorinen and Piironen 1984; McGowan and Davidson 1992), many of them related to human stocking practices and overfishing (Garcia de Leaniz and Verspoor 1989; Youngson et al. 1993; Castillo et al. 2008), which have destabilized the population structure in natural populations.

Hybridization offers a great opportunity to study the role of paternal effects in life history traits. Since the maternal contribution to fertilized eggs is much greater than the paternal contribution, few authors have assessed the relative importance of paternal effects during development and early life (Saillant et al. 2001; Probst et al. 2006). Maternal contribution to fertilized eggs is greater than that of the male, because sperm contain virtually no extra-nuclear material; therefore, any paternal-induced differences in life history traits are genetic in origin. In this study, we used a cross design that enabled us to establish the paternity of eggs in multiple sired clutches so that we could examine the paternal influence (strictly genetic) while avoiding confounding non-genetic factors associated with maternal effects linked to egg quality. This is possible because fish, like reptiles, yolk their follicles simultaneously and ovulate all the eggs at the same time; thus, energetic and nutritional within-clutch variance is very low compared with other oviparous groups, such as birds, that lay their eggs sequentially so that yolk composition can vary among eggs of the same clutch.

The goals of the present study were twofold. First, we experimentally crossed Atlantic salmon and brown trout in both directions of the cross (female salmon × male trout and female trout × male salmon) to address the mechanisms that explains the observed asymmetric hybridization between the two species. By doing so, we could assess if the absence of female salmon × male trout hybrids in the wild is the result of postzygotic barriers that produces embryonic selective mortality in one type of cross. Second, we analysed the incubation period of natural and hybrid crosses to assess the role of paternal effects in embryo development and the possible implications of early hatching on the fitness of the hybrids.

Materials and methods

Study animals and experimental design

The subjects of our study were wild Atlantic salmon (S) captured in the Río Cares (Asturias, Northwestern Spain) 2 months before spawning and hatchery brown trout (T, second hatchery generation) originating from the same river. On 21 December 2005, we made a split-plot factorial design cross involving six males and six females of each species. Both females and males were assigned to groups of four (two salmon and two trout). A sample of 10 eggs from each of the 12 females used in the experiment was measured (±0.01 mm) to control for maternal effects in development

rate. Each of the females' clutches was divided into four approximately equal portions, and each portion was mixed with milt from one of the four males. We added sperm in excess (>50 mL sperm per portion) to ensure that any difference in fertilization success among the four sires of a split brood was independent of initial differences in sperm concentration. This arrangement yielded 16 families, with each fish contributing to four of them. The split-plot design was replicated three times, obtaining a total of 48 families ($16 \times 3 = 48$ families: 12 ♀S × ♂S, 12 ♀T × ♂T, 12 ♀S × ♂T, and 12 ♀T × ♂S). Once the crosses were performed, approximately 300 eggs of each family were introduced into labeled flasks and transferred to the laboratory. Every family was held in a separate polyvinyl chloride (PVC) pipe with a plastic mesh bottom and incubated at a constant temperature (9 ± 0.1 °C). The incubation cylinders were fixed in one of two 200 L interconnected tanks with aerated recirculating water. Egg batches were randomly allocated to avoid tank effects, and all the crosses were equally represented in the two tanks. All the eggs that had not developed eyespots (stage 22; Vernier 1969) were considered unfertilized and were removed from the incubators. That approximation is frequently used to estimate fertilization success because 95% of the eggs that fail to reach this stage have developed identifiable visual signs of egg-white denaturation (unfertilized) within the first 2 days (Skarstein et al. 2005). All the white eggs were counted and removed to avoid possible fungus infections.

Once the first fry hatched, the number of individuals completely free from the egg envelope was counted every 8 h in each incubation cylinder to calculate time to hatching and estimate the time at which 50% of the embryos had hatched (H_{50}). H_{50} was fitted following the three-parameter hyperbolic model proposed for brown trout as the best fitting model at different temperatures (Elliott and Hurley 1998). After reaching development stage 27 (Vernier 1969; yolk absorption completed), the surviving fish of each family were transferred to 20 L individual trays provided with mesh windows and submersed in five interconnected 200 L tanks at 9 ± 0.1 °C. As in the previous stage, the trays were disposed randomly in the tanks, and all the crosses were equally represented in the four tanks. Fish were fed two times a day with commercial fish food (Trouvit 2, Trouw-E) and maintained in those conditions until the 16th week from fertilization when the experiment was terminated. All dead fry were removed and counted every day to have an estimation of mortality.

Statistical analysis

Three variables were analyzed in this experiment: relative fertilization success (RFS), defined as the percentage of eggs of each family that developed to eyed stage (stage 22; Vernier 1969); H_{50}, degree-days at which 50% of the surviving embryos had hatched (after removal of unfertilized eggs); and mortality, percentage of dead fish at the end of the experiment from the total fry that had hatched. Percentage data (RFS and mortality) were arcsin square-root transformed prior to analysis.

We used restricted maximum likelihood (REML) and a mixed model (e.g., Pinheiro and Bates 2000) to examine the effects of sire species (SireSp) and dam species (DamSp) in inter- and intra-specific crosses and to study the effect of sire (nested within SireSp) and Dam (nested within DamSp) on the RFS, H_{50}, and mortality. For the random effects (Sire, Dam, and the interactions Sire × DamSp, Dam × SireSp, and Sire × Dam (nested within SireSp × DamSp), the most reliable test is the likelihood ratio, which is computed taking the difference between the "–2 REML log-likelihood" of the model without the random effect and the full model (West et al. 2006). A model selection approach (Burnham and Anderson 1998) was used to compare all the possible models, the global model that includes fixed and random effects, and all possible interactions:

$$\begin{aligned} Y = {} & \text{SireSp} + \text{DamSp} + \text{Sire(SireSp)} \\ & + \text{Dam(DamSp)} + \text{SireSp} \times \text{DamSp} + \text{Sire(SireSp)} \\ & \times \text{DamSp} + \text{Dam(DamSp)} \times \text{SireSp} \\ & + \text{Sire} \times \text{Dam(SireSp} \times \text{DamSp)} \end{aligned}$$

and the other nine alternative models obtained by exclusion of one or various random factors and their interactions. We used the Akaike information criterion for small samples (AIC_c) to rank the candidate models and then evaluated model uncertainty with Akaike weights (w_i) (Burnham and Anderson 1998). Following the recommendations of Burnham and Anderson (1998), we used the model with lowest delta AIC score (Δ_i) as the best model to explain the data set. After selecting the best model, given the set of candidate models and the data, we discussed the significance of each term in the model in terms of p values. Model averaging was not used in the analyses because it would imply the consideration of complex models including some nonsignificant interactions with negligible biological effect.

To assess within-species variation in egg size in Atlantic salmon and brown trout, we used a nested analysis of variance (ANOVA) test in which each female was nested within their own species (S or T). To discard the maternal effects on developmental rate, we used analyses of covariance (ANCOVA) to test for among-crosses differences on the RFS. As in the previous analyses, we pooled the data of all the different crosses, and egg size was included as covariate. To complete the analyses, we used a one-way ANOVA to test the overall effects of the cross type on mortality. To do that analysis, we pooled the data of all the different crosses (♀S × ♂S, ♀T × ♂T, ♀S × ♂T, and ♀T × S). The analyses were conducted after verification of the assumption of homogeneity of variances with the Cochran's C test.

Results

The global model was not the best approximation of the data for any of the studied variables ($w_i > 0.0096$ and $\Delta_i > 5.25$ in all cases). A different model was used to analyze each dependent variable accordingly to their respective Akaike weights and Δ_i values (Table 1).

Relative fertilization success (RFS)

The type of cross had no significant effect on RFS (DamSp $F_{[1,29.576]} = 2.407$, $P = 0.131$; SireSp $F_{[1,10.184]} = 4.486$, $P = 0.06$; SireSp × DamSp: $F_{[1,29.576]} = 0.517$, $P = 0.478$). Both inter- and intra-specific crosses had a high fertilization success (mean RFS ± 1 standard error (SE); ♀S × ♂S = 84.16% ± 4.09%, ♀T × ♂T = 95.15% ± 4.09%, ♀S × ♂T = 93.49% ± 4.09%, ♀T × ♂S = 95.30% ± 4.09%;

Table 1. Summary of the model selection procedure for each of the three studied variables.

Model	–2log-likelihood	k	n	AIC_c	Δ_i	w_i
Relative fertilization success (RFS)						
RFS = DamSp + SireSp + Dam(DamSp) + Sire(DamSp) + DamSp × SireSp + Dam × SireSp*	339.029	7	49	348.054	0.00	0.3219
RFS = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp	342.654	6	49	349.254	1.20	0.17668
RFS = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp	339.029	8	49	350.608	2.55	0.08978
RFS = DamSp + SireSp + Dam(SireSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp + Sire × Dam(SireSp × DamSp)	339.029	8	49	350.608	2.55	0.08978
RFS = DamSp + SireSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Dam × SireSp + Sire × Dam(SireSp × DamSp)	339.029	8	49	350.608	2.55	0.08978
RFS = SireSp + DamSp + Dam(DamSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp +Sire × Dam(SireSp × DamSp)	339.047	8	49	350.626	2.57	0.08897
RFS = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp	339.047	8	49	350.626	3.63	0.05253
RFS = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp +Sire × Dam(SireSp × DamSp)	342.654	7	49	351.680	3.63	0.05253
RFS = SireSp + DamSp + Sire(SireSp) + Dam(DamSp) + SireSp × DamSp + Sire(SireSp) × DamSp + Dam(DamSp) × SireSp + Sire × Dam(SireSp × DamSp) (FULL)	342.654	7	49	351.680	5.25	0.02338
RFS = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp +Sire × Dam(SireSp × DamSp)	339.029	9	49	353.299	6.18	0.01466
Degree-days at which *50%* of the embryos hatched (H_{50})						
H_{50} = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp*	339.029	7	49	348.054	0.00	0.32193
H_{50} = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp	342.654	6	49	349.254	1.52	0.17668
H_{50} = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp	339.029	8	49	350.608	2.55	0.08978
H_{50} = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp +Sire × Dam(SireSp × DamSp)	339.029	8	49	350.608	2.55	0.08978
H_{50} = DamSp + SireSp + Dam(SireSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp + Sire × Dam(SireSp × DamSp)	339.029	8	49	350.608	2.55	0.08978
H_{50} = SireSp + DamSp + Dam(DamSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp +Sire × Dam(SireSp × DamSp)	339.047	8	49	350.626	3.44	0.08897
H_{50} = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp +Sire × Dam(SireSp × DtmSp)	342.654	7	49	351.680	3.94	0.05253
H_{50} = DamSp + SireSp + Dam(DamSp) + Sire(DamSp) + DamSp × SireSp + Dam × SireSp	342.654	7	49	351.680	3.94	0.05253
H_{50} = SireSp + DamSp + Sire(SireSp) + Dam(DamSp) + SireSp × DamSp + Sire(SireSp) × DamSp + Dam(DamSp) × SireSp + Sire × Dam(SireSp × DamSp) (FULL)	339.029	9	49	353.299	5.35	0.02338
H_{50} = SireSp + DamSp + Dam(DamSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp +Sire × Dam(SireSp × DamSp)	342.654	8	49	354.233	6.49	0.01466
Mortality (MORT)						
MORT = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp*	346.370	6	49	352.970	0.00	0.4444
MORT = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp	346.432	7	49	355.346	2.38	0.1355
MORT = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp +Sire × Dam(SireSp × DamSp)	346.370	7	49	355.396	2.43	0.1321
MORT = DamSp + SireSp + Dam(DamSp) + Sire(DamSp) + DamSp × SireSp + Dam × SireSp	346.370	7	49	355.396	2.43	0.1321
MORT = DamSp + SireSp +Dam(DamSp) +Sire(Sire Sp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp	346.370	8	49	357.949	4.98	0.0369
MORT = DamSp + SireSp + Dam(SireSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp + Sire × Dam(SireSp × DamSp)	346.370	8	49	357.949	4.98	0.0369
MORT = SireSp + DamSp + Dam(DamSp) + Sire(SireSp) + DamSp × SireSp + Sire × DamSp +Sire × Dam(SireSp × DamSp)	346.371	8	49	357.950	4.98	0.0368
MORT = SireSp + DamSp + Dam(DamSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp +Sire × Dam(SireSp × DamSp)	346.432	8	49	358.011	5.04	0.0357
MORT = SireSp + DamSp + Sire(SireSp) + Dam(DamSp) + SireSp × DamSp + Sire(SireSp) × DamSp + Dam(DamSp) × SireSp + Sire × Dam(SireSp × DamSp) (FULL)	346.370	9	49	360.641	7.67	0.0096
MORT = SireSp + DamSp + Dam(DamSp) + DamSp × SireSp + Sire × DamSp + Dam × SireSp +Sire × Dam(SireSp × DamSp)	358.458	8	49	370.037	17.07	0.0001

Note: Table shows the goodness of fit of each model (–2log-likelihood), number of parameters in the model (k), sample size (n), the Akaike information criterion for small samples (AIC_c), delta AIC scores (Δ_i), and the Akaike weights (w_i).

*The lowest Δ_i among the set of competing models.

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Fig. 1. Box plots of relative fertilization success (RFS). (*a*) RFS of families in non-hybrid and hybrid crosses (♀T × ♂T: brown trout non-hybrid crosses; ♀S × ♂S: Atlantic salmon non-hybrid crosses; ♀T × ♂S: hybrids between female brown trout and male Atlantic salmon; ♀S × ♂T: hybrids between female Atlantic salmon and male brown trout). (*b*) RFS for each one of the six dams of each species. (*c*) RFS for each one of the six sires of each species.

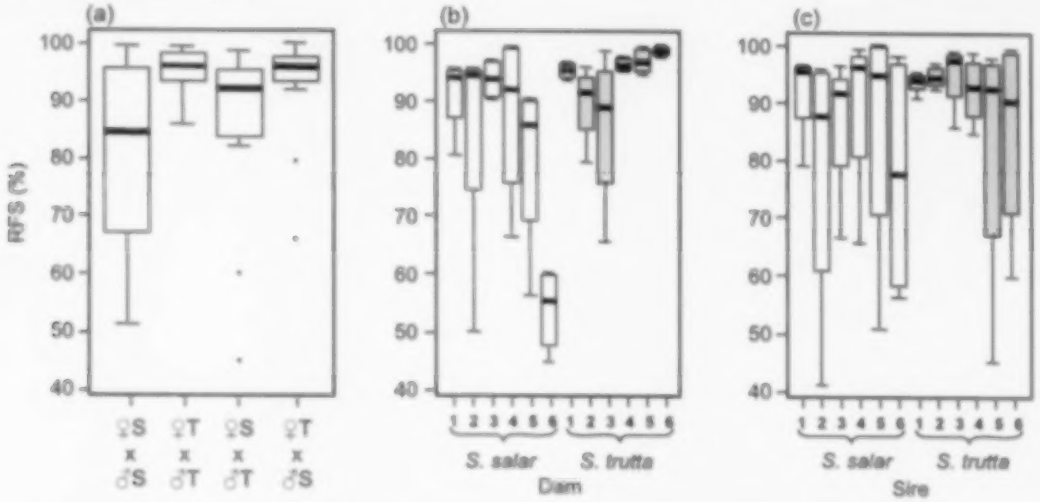


Fig. 1). We found a significant effect of the interaction DamSp × SireSp ($\chi^2 = 3.625$, $P = 0.0285$). That effect could be explained by differences in fertilization success in the crosses that involved one of the female Atlantic salmon (see Fig. 1, female salmon No. 6).

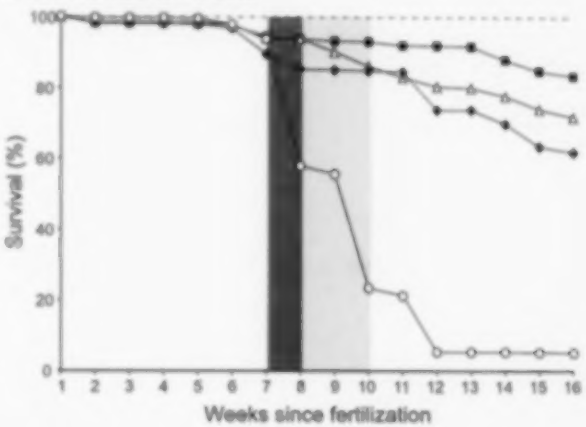
Results of the nested ANOVA indicated both significant differences in egg size between species ($F_{[1,108]} = 115.86$; $P < 0.00001$) and among females within species ($F_{[10,108]} = 15.32$; $P < 0.00001$). Despite those significant differences in egg size, the size of the egg had no significant effect on RFS (ANCOVA: $F_{[3,35]} = 21.950$; $P < 0.00001$).

Mortality

The type of cross had an important effect on mortality rates. There were significant effects of DamSp ($F_{[1,34]} = 245.549$, $P < 0.00001$) and the interaction DamSp × SireSp ($F_{[1,34]} = 198.319$, $P < 0.00001$) on the mortality from hatching until 16 weeks since fertilization. Moreover, we also found a significant effect of sire identity within each type of cross ($\chi^2 = 27.207$, $P < 0.00001$), indicating that mortality is dependent on the quality (and not just the species) of the father.

When we pooled the data of all the crosses, we found significant differences in mortality between crosses (ANOVA $F_{[3,44]} = 47.44$, $P < 0.00001$). The post hoc test demonstrated that differences in mortality between S intraspecific crosses and the interspecific crosses between dam S and sire T were nonsignificant (Tukey's honestly significant difference (HSD) test; $P = 0.92$; Fig. 2). On the other hand, when the sire was S and the dam was T, mortality was significantly higher than in the intraspecific crosses (Tukey's HSD test: ♀S × ♂T > ♀S × ♂S; $P = 0.0015$; Tukey's HSD test: ♀S × ♂T > ♀T × ♂T, $P = 0.0088$). The high mortality observed in the ♀T × ♂S hybrids mainly took place in the period between hatching and complete yolk absorption (7–10 weeks since fertilization; Fig. 2). At the end of the experiment (week 16), only 5.24% of the ♀T × ♂S hybrids remained alive, 30% of those hybrids showed skeletal malformations in their lower mandible (Fig. 3)

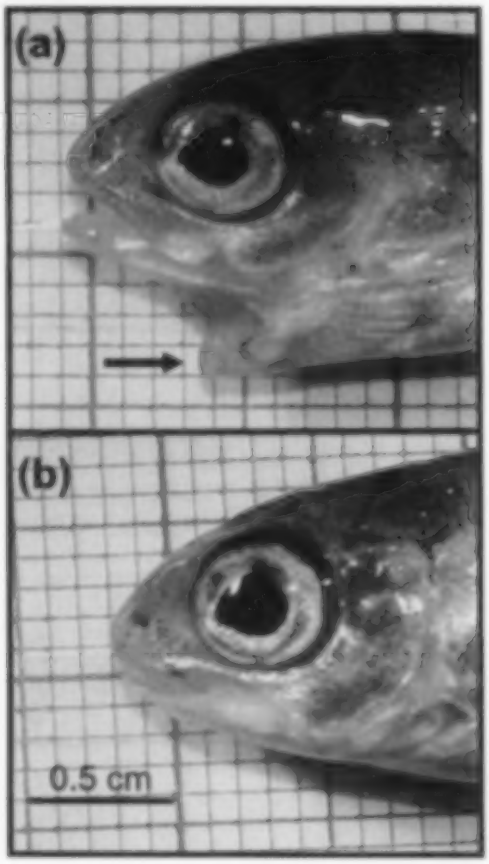
Fig. 2. Intrinsic hybrid viability as illustrated by the percentage of surviving embryos and fry as a function of developmental time until 16 weeks since fertilization. Dark grey area: hatching period; light grey area: yolk resorption period. ♀T × ♂T (-●-): brown trout non-hybrid crosses; ♀S × ♂S (-Δ-): Atlantic salmon non-hybrid crosses; ♀T × ♂S (-○-): hybrids between female brown trout and male Atlantic salmon; ♀S × ♂T (-◆-): hybrids between female Atlantic salmon and male brown trout.



Development time

Time to midhatch was strongly affected by the type of cross. We found significant effects of the DamSp ($F_{[1,9.244]} = 177.201$, $P < 0.000001$), the SireSp ($F_{[1,7.889]} = 57.677$, $P < 0.000001$), and the interaction DamSp × SireSp ($F_{[1,26.736]} = 8.681$, $P < 0.0065$). Intraspecific T embryos developed faster

Fig. 3. External deformity in the lower mandible (see arrow) in a hybrid between female brown trout and male Atlantic salmon (*a*) compared with a normal non-hybrid salmon of the same age (*b*). The bar scales indicate 0.5 cm.

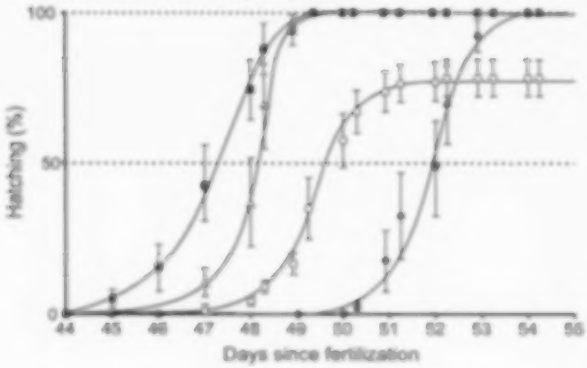


that S embryos (mean $H_{50} \pm 1$ SE; T: 423.1 ± 1.9 degree-days; S: 465.0 ± 1.9 degree-days; Fig. 4), and in the case of the hybrid crosses they showed an intermediate period of development between the two species. The significant effect of the interaction SireSp × DamSp ($\chi^2 = 3.94$, $P = 0.0236$) demonstrated a paternal effect in embryo development, showing that hybrid crosses with sire T and dam S developed faster (♀S × ♂T H_{50} = 432.1 ± 1.9 degree-days) that those hybrids with dam T and sire S (♀T × ♂S H_{50} = 448.2 ± 1.9 degree-days) (Fig. 4). A high percentage (~20%) of the ♀T × ♂S hybrids never hatched, although they had apparently completed development up until that stage.

Discussion

The results of the present study support the idea that both hybrid viability and differences in development time are important factors explaining asymmetric hybridization between S and T. Previous studies carried out in the same study area with these species assumed that differences in occurrence of both types of hybrids (♀T × ♂S and ♀S × ♂T) in the wild could be due to prezygotic behavioural mechanisms that favoured one direction of the cross and hindered the opposite direction (Garcia-Vazquez et al. 2002, 2004; Gephard et al. 2000). Our results demonstrated for the first time that contrary to that hypothesis, high mortality of ♀T × ♂S hybrids before yolk absorption is the main factor to explain the observed asymmetric hybridization in the study area.

Fig. 4. Development time. Cumulative percentage of families in non-hybrid and hybrid crosses and intercrossed line to midhatch (50% hatching). ♀T × ♂T (-●-): brown trout non-hybrid crosses; ♀S × ♂S (-△-): Atlantic salmon non-hybrid crosses; ♀T × ♂S (-○-): hybrids between female brown trout and male Atlantic salmon; ♀S × ♂T (-◆-): hybrids between female Atlantic salmon and male brown trout. Horizontal dashed lines at 50% and 100% indicate time of midhatch and full hatching, respectively.



Several processes are involved in reproductive isolation between sympatric salmonid species, such as behavioural differences, use of habitat, secondary sexual traits, or size of maturation (Taylor 2004). In Pacific species, it is common for differences in age of maturity or nest site selection to limit the opportunities for hybridization. For example, sockeye salmon (*Oncorhynchus nerka*) is the only species of *Oncorhynchus* that spawn in submerged gravel beaches in the bottom of the lakes, and this behaviour prevents hybridization with sympatric species, like the Chinook salmon (*Oncorhynchus tshawytscha*), which makes important upstream migrations to spawn in small shallow streams (Taylor 2004). Differences in size of maturation among similar species can constrain hybridization, but in some circumstances such differences may promote hybridization, such as for sneaking behaviour. For instance, in south European rivers, S and T often share their breeding grounds, and parr sneakers parasitize breeding pairs of T and S. Although the high aggressiveness of T males towards sneaking male S parr (Bremset and Heggenes 2001; Garcia-Vazquez et al. 2001) could reduce their breeding success, the contribution of sneaking S to hybrid crosses is expected in the studied area. Moreover, small male T can become sneakers and fertilize the eggs of spawning S (D. Álvarez, unpublished data). One hypothesis proposed to explain the observed asymmetric hybridization in salmonids involves sneak spawnings by males of the smaller species. For example, where Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) are sympatric, Dolly Varden mature at smaller sizes than bull trout, and in this case hybridization occurs in the direction of male Dolly Varden × female bull trout (Taylor 2004). In our study system, S sneakers mature at smaller sizes than T, and according to

the predictions of that hypothesis, we would expect that the direction of hybridization were male S × female T. Therefore, changes in Atlantic salmon population during the last decades and sneaking behaviour could have relaxed the premating barriers between the two species, consequently resulting in the increase of interspecific crosses.

If prezygotic barriers to hybridization are circumvented, eggs can potentially reject heterospecific sperm and avoid fertilization (O'Rand 1988). Our results have demonstrated the apparent absence of that rejection, since fertilization success was similar in both intra- and inter-specific crosses, and this excludes the gametic selection explanation, which proposes a difference in the fertilization success between heterospecific and homospecific sperm.

Despite the similarity in fertilization success, embryonic mortality in the later stages of development was almost total (mortality rate = 95%) in the ♀T × ♂S crosses, whereas the reciprocal cross had normal development and mortality rates similar to those in intraspecific crosses. Significant parental interactions may indicate a form of incompatibility among parents. This interpretation is supported by the results of our analyses, revealing that the significance of maternal and paternal effects depended on the cross combination. Because F_1 hybrids in the two reciprocal crosses have the same nuclear DNA and chromosome content (one complete set of chromosomes of each species), mortality in female trout × male salmon crosses could involve incompatibility between T maternal cytoplasm and S paternally inherited genes (Turelli and Moyle 2007). Another possible explanation for unequal mortality in the two types of crosses could be differences in sex-linked sequences, that is, DNA associated to the factor that determines male development of embryos. The sex-determining loci (Y chromosome, females being homogametic) are preserved on homologous, but different, autosomal linkage groups in S and T (Woram et al. 2003). However, a small region of DNA has been involved in the rearrangement of the sex-determining region as revealed by molecular markers adjacent to the sex-determining loci (Artieri et al. 2006); thus, the last explanation does not seem plausible to explain asymmetric survival of embryos issued from opposite cross directions.

However, as our results have demonstrated, the low survival of ♀T × ♂S hybrids during the first stages of development could explain the absence these hybrids in the wild. Mortality took place mainly in the late stages of development, when embryos were almost completely developed, and even fry that hatched often died before the full resorption of yolk sac, perhaps because of deformities that would make difficult the liberation of the fry from the eggshell. Our results showed that 30% of the hybrids that survived that stage showed external deformitie,s and those deformities might compromise feeding ability and therefore survival in the wild;however, we do not have empirical support for this supposition.

It has been demonstrated that asymmetric hybridization may be due to embryonic mortality during the first phases of development. In some combinations of interspecific crosses among different species of rhabditid nematodes, embryos were not viable and arrested prior to gastrulation (Baird et al. 1992). That hybrid lethality is consistent with the presence of a lethal factor in maternal cytoplasm, as has been observed in *Drosophila* (Hutter et al. 1990). Thus, there may be a common genetic basis for hybrid lethality in a wide range of genera. In our case, it does not seem to have the same kind of embryonic lethality because the resulting embryos between ♀T and ♂S developed beyond gastrulation, but it is reasonable to think that incompatibility of T mtDNA with the S nuclear genome may render hybrids from T mothers unviable or at least could produce abnormalities and mortality in later stages of development. In contrast, ♀S × ♂T hybrids experienced development and mortality rates similar to the intraspecific crosses of the two species, suggesting that in this case those incompatibilities between female mtDNA and male nuclear genome do not exist. Therefore, the presence of that last type of hybrids in the wild is consistent with the absence of postzygotic barriers between the two species in this direction of the cross (Wilkins et al. 1993; Galbreath and Thorgaard 1995). Moreover, interspecific mating between S females and T males has been confirmed in the wild in several occasions (Jansson et al. 1991; D. Álvarez, personal observations), involving T sneakers that parasitize S pairs and also matings between large T males and S females. Those matings involving large trout males must be frequent because of the very aggressive behaviour of those fish in the spawning grounds (Bremset and Heggenes 2001; García-Vázquez et al. 2002). In this case, the rupture of the premating barriers between the two species could have been affected by human causes, such as overfishing and stocking practices (McGowan and Davidson 1992). One of the curiosities of the hybridization between S and T is the observed differences in maternal contribution in different parts of the distribution; while in Europe the mothers are the salmon, in North America the mothers are the trout. Those differences could be related by the fact that brown trout is an introduced species in North America, whereas in Europe both species are sympatric.

Another important finding of the present study is the existence of paternal factor in embryo development. Development time is variable in fishes and is mainly related to the maternal contribution that can be either genetic or phenotype-based (i.e., yolk). Egg size and yolk composition can influence development time, embryonic survival, and size at hatch in ectotherm vertebrates (Johnston et al. 2007). In our case, we have demonstrated that although T eggs were significantly smaller than S eggs, these differences in size have no effect on development time among experimental crosses. Recent research has confirmed the role of paternal effects in some of those early life history traits (Olsson et al. 1996; Granath et al. 2004), and hence it seems that such traits are under genetic control. Among salmonid species, there are strong differences in development time, and even within the same species it has been demonstrated that local adaptation strongly influences it. For example, Sockeye salmon embryos from colder environments require fewer days to hatch than embryos from warm environments when eggs were incubated in a common environment (Beacham and Murray 1989), and in coho salmon (*Oncorhynchus kisutch*) three different populations derived from isolated wild populations showed differences of more that 15 days in time to midhatching and intermediate development time of intercrossed hybrids with respect to those control lines (Granath et al. 2004).

Brown trout embryos required fewer days to develop than Atlantic salmon embryos, and our results showed that

development times of interspecific hybrids were intermediate to those of intraspecific crosses. Once we excluded the effect of egg size on developmental rate, we confirmed that sire species had a strong effect on development, since hybrids between male trout and female salmon developed faster than intraspecific salmon crosses, and hybrids between male salmon and female trout developed slower than intraspecific trout crosses. A similar pattern has been observed in spadefoot toads, *Spea bombifrons* and *Spea multiplicata*, which co-occur in the southwest of United States and hybridize frequently (Pfennig and Simovich 2002). In those species, *S. multiplicata* develop faster than *S. bombifrons*, and hybrid tadpoles between female *S. bombifrons* and male *S. multiplicata* develop sooner than non-hybrid *S. bombifrons* tadpoles (Pfennig and Simovich 2002). In this case, hybridization by *S. bombifrons* females results in a trade-off whereby hybrid offspring will have lower fertility and fecundity, but they will develop faster than pure *S. bombifrons* offspring, and therefore they will have more chances to escape a drying pool (Pfennig and Simovich 2002).

Changes in hatching times could have repercussions later in development, and factors like time of emergence or size at hatch can have a profound effect on survival and later reproduction because of factors such as prior residence effects (e.g., Velando 2000; Metcalfe et al. 2003; Drummond 2006) because early emerging fry tend to be dominant and have a competitive advantage to later emerging fry (Metcalfe and Thorpe 1992), which as a result may have slower growth rates. In S, prior residents do not only monopolize the best feeding sites, but also they win the majority of the aggressive interactions, and thus they achieve higher feeding rates (Harwood et al. 2003). Huntingford and Garcia de Leaniz (1997) have shown that 1 day is sufficient for a prior residence effect to be evident in S parr; therefore, differences in hatching time of 3–4 days as we have recorded between hybrids and non-hybrids could determine dominance hierarchies in gravel. Our results suggest that because of the early emergence of ♀S × ♂T hybrids with respect to the pure Atlantic salmon, they could arrive first on the feeding grounds and hence could become more dominant and will develop faster than those that had been fertilized at the same time.

Hybridization between salmonids is usually due to anthropogenic reasons. Sometimes, humans introduced exotic species, which adapt to their new habitats and may hybridize with local species (Bernatchez et al. 1995; McGowan and Davidson 1992), and in other cases the excessive pressure on a species can destabilize the fish community and promote asymmetric hybridization, as happens in the north of Spain, where S populations are small and declining, whereas T populations are large and stable (Reyes-Gavilán et al. 1996). In this case, as females of the rare species wait upon the spawning grounds for intraspecific mates, they become less discriminating and may eventually mate with males of a more common species (Wirtz 1999). The consequences of hybridization between salmonids may be extremely serious. Studies of captive fish have revealed that S × T hybrids can be fertile and their offspring can be viable (Wilkins et al. 1993; Galbreath and Thorgaard 1995). In the north of Spain, it has been reported that hybridization can lead to genetic introgression between the two species (Castillo et al. 2007, 2008). This was also confirmed in other salmonid species, for example, Bernatchez et al. (1995) demonstrated introgression of Artic char (*Salvelinus alpinus*) mtDNA into several populations of brook trout (*Salvelinus fontinalis*) in eastern Quebec. Apart of the genetic effect of hybrids on natural populations, hybrids could cause a further reduction of Atlantic salmon spawning success through backcrossing, as well as through competition for mates and spawning sites.

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Life history variation in upper Columbia River Chinook salmon (*Oncorhynchus tshawytscha*): a comparison using modern and ~500-year-old archaeological otoliths

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Abstract: Conservation planning often occurs only after a species has been extirpated from portions of its historical range and limited information is available on life history diversity prior to development. To provide information on Chinook salmon (*Oncorhynchus tshawytscha*) life history before and after local extirpation, we examined the chemical (^{87}Sr:^{86}Sr, Sr:Ca) and structural composition of modern and archaeological otoliths from the upper Columbia River. We compared otoliths from modern spring (yearling migrant, $n = 15$) and summer–fall (yearling ($n = 7$) and subyearling ($n = 12$) migrants) runs with those from extirpated runs ($n = 8$) to estimate the number of and similarity among natal environments and reconstruct aspects of the migratory history. Presumptive natal sources were most similar between the archaeological collections and the modern summer–fall run. Chinook salmon represented by the archaeological otoliths also displayed life history traits, including size at freshwater emigration and adult size at return to fresh water, most similar to the summer–fall subyearling run. These data indicate that there is the potential to maintain aspects of predevelopment Chinook salmon life histories in the Columbia River, and strategies that promote maintenance of that life history diversity may be warranted.

Résumé : La planification de la conservation se produit souvent seulement une fois qu'une espèce a été éliminée de plusieurs parties de son aire historique et qu'il n'existe plus que peu d'information sur la diversité des cycles biologiques d'avant le développement économique. Afin d'obtenir des informations sur le cycle biologique de saumons chinook (*Oncorhynchus tshawytscha*) avant et après leurs extirpations locales, nous avons analysé la composition chimique (^{87}Sr:^{86}Sr, Sr:Ca) et structurale d'otolithes modernes et archéologiques provenant du cours supérieur du fleuve Columbia. Nous avons comparé les otolithes des montaisons modernes du printemps (migrateurs d'un an, $n = 15$) et de l'été–automne (migrateurs d'un an, $n = 7$ et de moins d'un an, $n = 12$) à des otolithes provenant de montaisons éliminées ($n = 8$) afin de déterminer le nombre de milieux d'origine et la similarité entre eux et de reconstituer certains aspects de l'histoire de la migration. Les milieux d'origine présumés sont plus semblables entre les collections archéologique et les montaisons modernes d'été–automne. Les saumons chinook représentés par les otolithes archéologiques présentent aussi des traits de cycle biologique, et en particulier la taille à l'émigration depuis l'eau douce et la taille adulte lors du retour en eau douce, plus semblables à ceux de la montaison d'été–automne des poissons de moins d'un an. Ces données indiquent qu'il existe une possibilité de maintenir certains aspects des cycles biologiques des saumons chinook du Columbia d'avant le développement économique et qu'il y aurait lieu de mettre en place des stratégies qui favorisent le maintien de la diversité des cycles biologiques.

[Traduit par la Rédaction]

Introduction

Effective management and conservation of biological populations relies on accurate classification of existing genetic, ecological, and life history diversity. However, conservation planning often commences only after a species has been extirpated from portions of its historical range and limited information is available on life history variation prior to development. Although phenotypic variation can be challenging to quantify and conserve, it may be critical for the maintenance of certain populations (Conover et al. 2006). Furthermore, as local adaptation and selection can occur

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over relatively short time scales (Hendry and Kinnison 1999; Unwin et al. 2000; Connor et al. 2005), determining whether substantial life history variation has been lost is highly relevant to conservation efforts. Therefore, we completed a preliminary analysis to determine the feasibility of reconstructing aspects of life history variation in an extirpated population of Chinook salmon based on archaeological otolith collections.

Chinook salmon (*Oncorhynchus tshawytscha*) is an anadromous species that has been extirpated from ~40% of its historical freshwater range in the contiguous USA (Gustafson et al. 2007). In the Columbia River Basin, which is the second largest watershed in the USA, extensive habitat and population loss has occurred because of hydropower development and landscape modifications. Chinook salmon currently spawn up to Chief Joseph Dam (47°59′N, 119°38′W), which is 877 km from the mouth and marks the upstream extent of contemporary salmon distribution. Historically, there were >500 km of potential salmon habitat accessible upstream of the dam (Fulton 1968).

Evolutionarily significant units (ESUs), which are based on genetic, ecological, and life history diversity, are used to classify diversity in biological populations in the USA (Waples et al. 2001; Gustafson et al. 2007). Currently, there are 17 ESUs established for Chinook salmon throughout the contiguous USA and two within the upper Columbia River (Myers et al. 1998): (*i*) the upper Columbia River spring run, which is listed as endangered under the Endangered Species Act (Good et al. 2005); and (*ii*) the upper Columbia River summer–fall run. The run time (spring vs. summer–fall) refers to the season during which adults return to their natal rivers for reproduction. In general, the spring run displays a yearling life history, where juveniles emigrate from fresh water after 1 year, whereas the summer–fall run displays a subyearling life history, where juveniles emigrate from fresh water during their first year and tend to reside longer in estuaries and coastal habitats (Healey 1991). However, both juvenile migratory behaviors can occur in either run (Myers et al. 1998). Additionally, runs with yearling life histories typically display smaller adult body size-at-age compared with runs with subyearling life histories (Healey 1991).

Large numbers of salmon are produced in hatcheries to compensate for loss of habitat within the Columbia River. For example, >100 million hatchery-produced spring and summer–fall run Chinook salmon from upper Columbia River stocks were released between 1999 and 2008 (Regional Mark Processing Center: http://www.rmpc.org/). Hatcheries release primarily larger, older individuals; such practices can promote the dominant tactic, or phenotype, and reduce life history variation within a population, which may in turn reduce population resiliency (Healey 2009). Currently, there is minimal information about whether substantial life history variation has been lost in these populations and whether contemporary life history traits are representative of predevelopment populations.

Our capacity to determine life history traits retrospectively has expanded with the development of biogeochemical markers. Elemental and isotopic analyses of biological structures have been used to reconstruct aspects of an individual's life history, including determination of provenance and migration patterns in humans (Hedman et al. 2009), birds (Hobson 1999), woolly mammoths (Arppe et al. 2009), and fishes (Koch et al. 1992; Campana 2004; Dufour et al. 2007). For fishes, otoliths provide an excellent forensics tool because they grow continuously, display no evidence of resorption, and record high frequency (daily) aspects of the environment in which a fish resided. Examination of otolith strontium (^{87}Sr:^{86}Sr and Sr:Ca) has been used to determine provenance (Kennedy et al. 1997; Ingram and Weber 1999) and reconstruct movement patterns and migration histories in both Pacific (Zimmerman et al. 2003; Miller et al. 2010*a*; Volk et al. 2010) and Atlantic (*Salmo salar*) salmon (Kennedy et al. 2002). These approaches are based on positive relationships between otolith and water strontium composition (Kennedy et al. 1997; Zimmerman 2005).

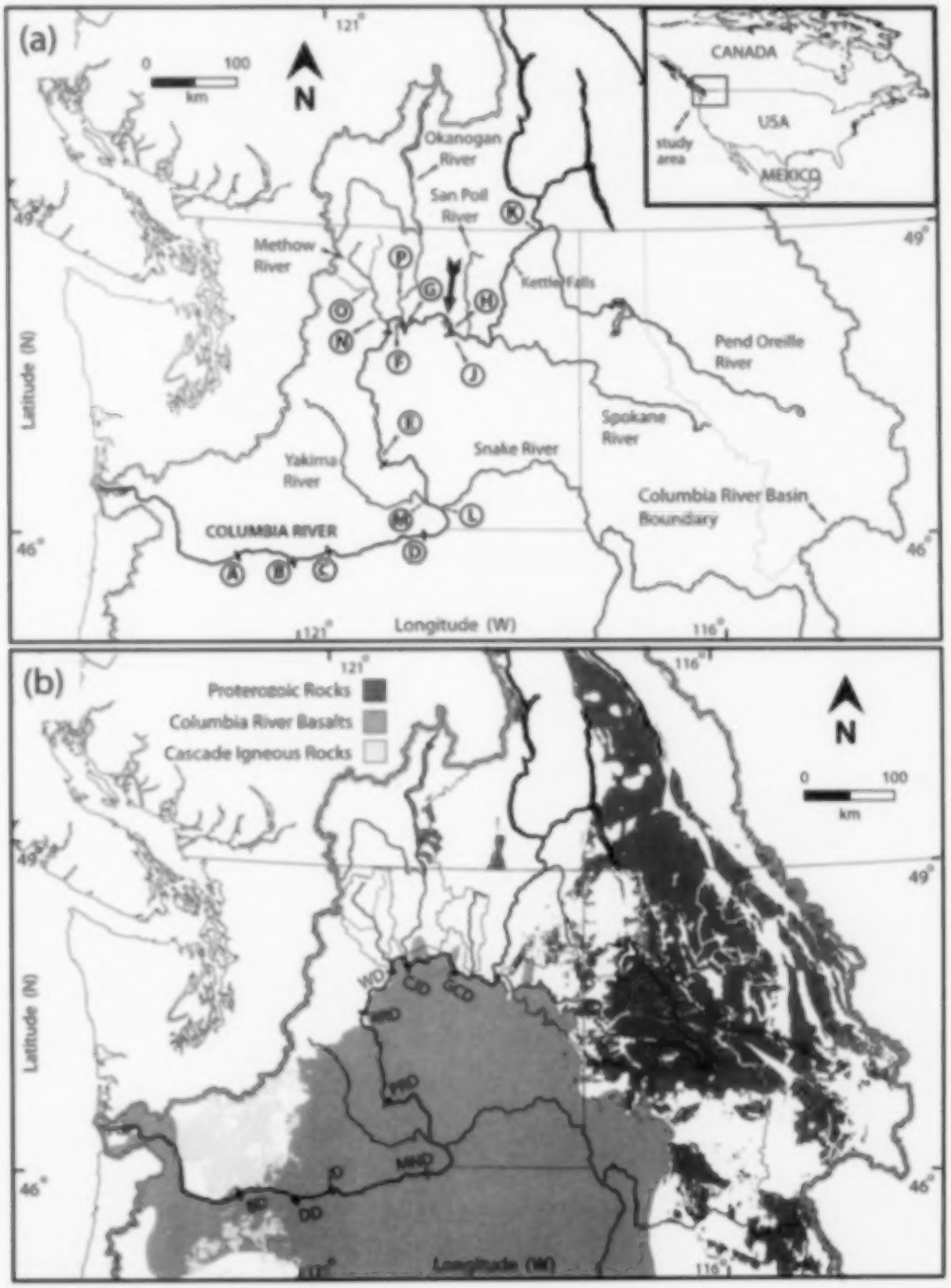
We obtained otoliths from modern and extirpated populations of Chinook salmon in the upper Columbia River Basin to determine if we can reconstruct aspects of this species' life history. The direct comparison of individuals from the same geographic region before and after non-indigenous human settlement and hydropower modification would provide empirical evidence on life histories prior to widespread human impacts. We based our approach on otolith chemical (^{87}Sr:^{86}Sr, Sr:Ca) and structural analyses because otoliths provide a chemical record adequate to differentiate between fresh and marine waters and among freshwater systems and growth structures amenable to robust back-calculation of individual size (Francis 1990). Our primary study objectives were to (*i*) estimate the number of and similarity among natal environments and (*ii*) reconstruct aspects of the life history, including determination of size at freshwater emigration, life history type (yearling vs. subyearling), and adult body size upon return to fresh water. Additionally, we assessed the archaeological otoliths for evidence of diagenesis, which refers to any chemical or physical change after initial deposition. There can be partial to complete exchange of the original elemental constituents with locally derived sources; extensive diagenesis could remove the original Sr record and lead to an uninterpretable pattern of Sr within the otolith.

Materials and methods

Modern otolith collection

Sagittal otoliths from Chinook salmon spawners representative of current runs were obtained in 2007 by Washington Department of Fish and Wildlife (WDFW) personnel. Individuals from the spring (n = 15) and summer–fall (n = 19) runs were collected at the Wells Dam and Hatchery facilities (47°57′N, 119°52′W) (Fig. 1). Individuals were assigned to one of these two seasonal runs based on the time of collection and verified with genetic analysis (Seeb et al. 2007; C. Snow, WDFW, 20268 Highway 20, Suite 7, Twisp, Washington, unpublished data). Most hatchery fish could be visually identified because all yearling and many of the subyearling fish had their adipose fin clipped prior to release as juveniles. WDFW personnel also collected information on fork length (FL, cm) and classified fish as hatchery or naturally spawned based on scale analysis (e.g., Connor et al. 2005). We wanted to compare naturally occurring life history variation in modern runs with our archaeological collections; therefore, we only included fish that were classified as naturally spawned based on scale analysis. The naturally spawned

Fig. 1. Map of Columbia River and tributaries. (*a*) Majority of the Columbia River watershed, including the Snake, Yakima, Methow, Okanogan, San Poil, Pend Oreille, and Spokane rivers. Locations where riverine $^{87}Sr/^{86}Sr$, Sr (ppb), and Sr:Ca (mmol·mol^{-1}) data were collected are identified by letters (data are presented in Table 1). Approximate location of archaeological site is indicated by black arrow. (*b*) Distribution of major rock units in the Columbia River watershed, including Cascade Igneous rocks (mean $^{87}Sr/^{86}Sr \pm 1$ standard deviation (SD) = 0.7034 ± 0.0004, n = 99); Columbia River Basalt Group ($^{87}Sr/^{86}Sr$ = 0.7046 ± 0.0010, n = 224); and Proterozoic rocks ($^{87}Sr/^{86}Sr$ = 0.8847 ± 0.1028, n = 77). Mainstem dams, including Bonneville (BD), The Dalles (DD), John Day (JD), McNary (MND), Priest Rapids (PRD), Rocky Reach (RRD), Wells (WD), Chief Joseph (CJD), and Grand Coulee (GCD), are identified.



individuals from the spring run likely originated within the Methow River Basin, whereas those from the summer–fall run likely originated within the Methow or Okanogan river basins (Fig. 1) (C. Snow, WDFW, 20268 Highway 20, Suite 7, Twisp, Washington, personal communication, 2009). Prior to the construction of Grand Coulee Dam in 1942, Chinook salmon were intercepted on their upstream migration, spawned, and their offspring released into tributaries below the future dam location as part of the Grand Coulee Fishery Maintenance Project (Myers et al. 1998). Therefore, modern runs in this region may have been influenced by introgression as a result of these introductions.

Archaeological site and otolith collection

The archaeological site (site No. 45-DO-285) (Fig. 1*a*), which is located above Chief Joseph Dam, was excavated in 1978–1980 prior to expansion of the dam and subsequent pool rise. The site is located on the west bank of the Columbia River in Douglas County, downriver of Grand Coulee Dam. Specific site location information is withheld given tribal concerns. The site was occupied from 3000 to 250 years BP, and most of the site's fish remains were recovered from the most recent occupation zone, dating between 250 and 500 years BP (Miss et al. 1984). The fish assemblage is dominated by otoliths from Chinook salmon; bony specimens of the cranium and vertebral column are extremely uncommon. The scarcity of cranial bony specimens probably results from deterioration after deposition. Vertebrae are extremely robust, however, and their absence more likely is because carcasses were not deposited at the site (Butler 1990). Previous researchers suggest that the most recent occupation represents a seasonally occupied fishing camp rather than a village (Miss et al. 1984). Salmon were likely procured at a nearby rapid (now drowned by the reservoir) and then brought to the site where heads were cut off and deposited while the remainder of the carcass was taken elsewhere (Butler 1990). Such butchering–processing activities are known for numerous Native American groups throughout the Pacific Northwest (see references in Butler and Chatters 1994). The particular season of fishery activities is difficult to estimate from existing archaeological records (Miss et al. 1984). According to local ethnographic records obtained in the 1920s, "salmon is present in the middle Columbia from May until November" (Ray 1933, p. 57); salmon represented in the archaeological site could have been taken any time in that period.

We obtained permission to analyze ten sagittal otoliths from Chinook salmon (identified using Casteel 1974) collected from the site. To determine life history characteristics of fish closest in age but prior to the time of major hydropower development and in-channel modifications, we selected otoliths from the most recent occupation zone (250–500 years old) (Miss et al. 1984).

Otolith preparation and elemental analyses

Sagittal otolith thin sections were prepared using established protocols for element analysis (e.g., Miller 2009). Otolith elemental and isotopic data were collected along transects that intersected the otolith core (Figs. 2*a*, 2*c*). We collected ^{87}Sr:^{86}Sr and Sr:Ca data from 21 modern (n = 10 for spring yearling; 5 for summer–fall yearling; and 6 for summer–fall subyearling migrants) and 8 of the 10 archaeological otoliths (two were damaged during preparation). We collected only ^{87}Sr:^{86}Sr data from the remaining 13 modern otoliths (n = 5 for spring yearling; 2 for summer–fall yearling; and 6 for summer–fall subyearling migrants).

To quantify otolith ^{87}Sr:^{86}Sr, we used a NuPlasma multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS) and a New Wave DUV193 excimer laser. We followed the general method of Woodhead et al. (2005) as described in Miller and Kent (2009) to correct for potential Kr and Rb interferences and monitor for Ca argide–dimer formation. The laser was set at a pulse rate of 10 Hz with a 40 μm ablation spot size and travelled at 2 μm·s^{-1}. Data were collected across the otolith growth axis to generate a life history profile; data were generated in blocks composed of two, 2 s cycles and represent the average value across 8 μm of the otolith. To assess instrument accuracy, we determined the ^{87}Sr:^{86}Sr of a marine gastropod (= 0.70918) and consistently obtained a mean value (±2 standard errors, SE) of 0.709291 ± 0.000008 (n = 18); otolith ^{87}Sr:^{86}Sr values were corrected for this difference.

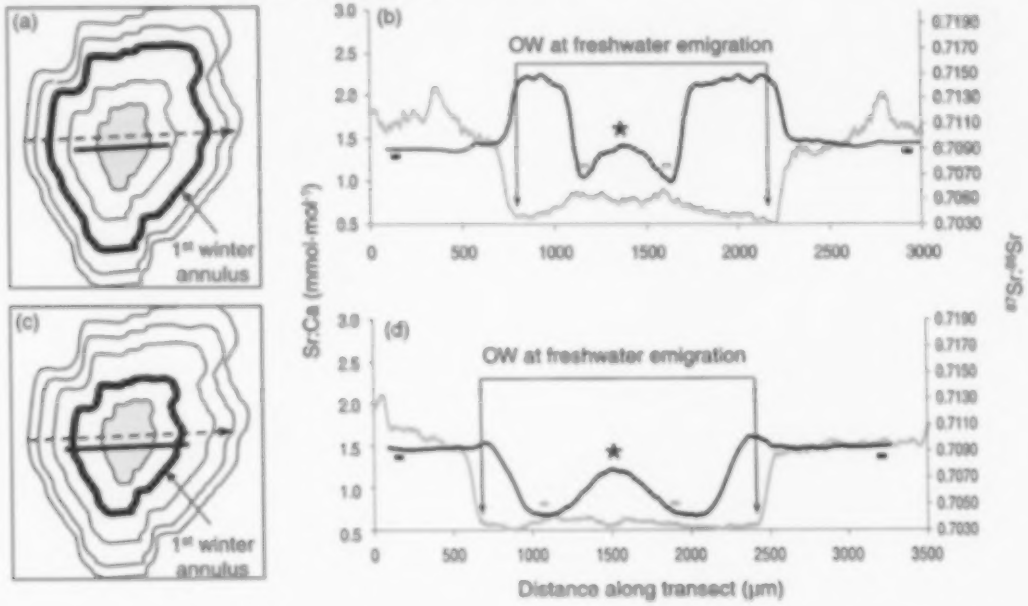
To quantify otolith Ca and Sr concentrations along the otolith growth axis, we used a VG PQ ExCell ICP-MS (Thermo Scientific) with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 15 Hz with a 40 μm ablation spot size and travelled at 5 μm·s^{-1}. Normalized ion ratios were converted to molar ratios based on our measurements, known average elemental concentrations of National Institute of Standards and Technology (NIST) 612 glass standards, and molar mass of Ca and Sr. Limits of detection (ppm) were calculated as three standard deviations (SDs) of background measurements: Ca = 0.07, Sr = 0.09. The mean percent relative SDs for glass standards were ^{43}Ca = 2.6% and ^{88}Sr = 5.6%. A calcium carbonate standard prepared by the United States Geological Society (USGS MACS-1) provided an estimate of accuracy (99% for Sr:Ca).

Natal sources

Spatial variation in riverine values of ^{87}Sr:^{86}Sr, which reflect the age and mineralogy of the surrounding geology, can be used to differentiate among natal environments in anadromous fishes (Kennedy et al. 1997, 2002). ^{87}Sr is produced by the radioactive decay of ^{87}Rb; rocks of the continental crust (e.g., granites) are relatively high in rubidium, whereas rocks typical of oceanic crust (e.g., basalts) have much lower concentrations (Faure 2001). Because the half-life of ^{87}Rb is on the order of 49 billion years, very old continental rocks, sedimentary rocks eroded from very old continental crust, or younger igneous rocks contaminated when passing through very old continental crust will have accumulated more ^{87}Sr and have higher ^{87}Sr:^{86}Sr ratios than oceanic crust and some surface basalt flows.

The Columbia River Basin drains a large (~660 500 km^2) and geologically complex area that provides an opportunity to examine natal sources using ^{87}Sr:^{86}Sr (Fig. 1*b*). We separated the region into dominant rock assemblages and associated chemical signatures. Rocks with the highest ^{87}Sr:^{86}Sr values (typically >0.7199) are found in the northern and eastern ends of the basin and are derived from Proterozoic basement rock (Obradovitch and Peterman 1968; Criss and Fleck

Fig. 2. (*a*) Schematic (sagittal section) of a sagittal otolith of an adult summer–fall run subyearling Chinook salmon. Dashed line indicates laser path for elemental analysis and solid line represents otolith width (OW) at freshwater emigration. The maternally influenced region of the otolith, which represents the egg and very early juvenile life history, is shaded and the first winter annulus is labelled. (*b*) Sr:Ca (mmol·mol^{-1}) (gray line) and ^{87}Sr:^{86}Sr (black line) across an otolith from an adult summer–fall run, subyearling Chinook salmon. Measurement of OW (μm) at freshwater emigration is identified. The asterisk identifies the maternally influenced region of the otolith; the gray dashes identify the region across which ^{87}Sr:^{86}Sr was averaged to characterize natal source; and the black dashes identify the region across which ^{87}Sr:^{86}Sr was averaged to characterize marine residence. (*c*) Schematic of sagittal otolith from an adult spring run yearling Chinook salmon. Annotations are the same as in (*a*). (*d*) Sr:Ca (mmol·mol^{-1}) (gray line) and ^{87}Sr:^{86}Sr (black line) across an otolith from an adult spring run yearling Chinook salmon. Annotations are the same as in (*b*).



1987). Rocks that underlie the central and western portions of the Basin are parts of terranes accreted to the western edge of North America during the Mesozoic Era. Each terrane has a geologic history that is distinct from its neighbor until they are amalgamated and (or) pushed up against the North American (NA) craton (i.e., a stable portion of a continent that forms the central mass of the continent).

As groups of terranes were accreted to the NA craton, they were commonly stitched together by plutons (i.e., intrusive igneous rocks associated with a subduction zone). Studies of these Mesozoic- and Cenozoic-age plutons and their eruptive equivalents report ^{87}Sr:^{86}Sr values <0.7210, and the ratio generally decreases from east to west with distance away from the edge of the NA craton (Armstrong et al. 1977; Carlson et al. 1981; Armstrong 1988). The boundary between Proterozoic basement and accreted basement rocks in north–central Washington State is approximated by the Okanogan River, the likely source of the modern summer–fall run samples included in this study. Much of the central and western portions of the basin were subsequently covered by the Columbia River Basalts (Fig. 1*b*), which erupted between 17 and 6 million years ago and have average ^{87}Sr:^{86}Sr values of 0.7046 in central Washington (Ramos et al. 2005) but higher values (~0.7060–0.7145) for the youngest flows erupted near the tri-state corner of Oregon, Washington, and Idaho (McDougall 1976; Hooper and Hawksworth 1993; Brandon and Goles 1995). To the west of the Columbia River Plateau basalts, the river passes through the High Cascades region where rocks associated with Eocene to Pleistocene age volcanoes (Cascade Igneous Rocks in Fig. 1*b*) have average ^{87}Sr:^{86}Sr values around 0.7039 (Hedge et al. 1970; Church and Tilton 1973; Schmidt et al. 2008).

Overall, the geologic data indicate that the waters of the upper reaches where the modern and extirpated Chinook salmon in our study originated span a broad range of ^{87}Sr:^{86}Sr values (Wadleigh et al. 1985; Goldstein and Jacobsen 1987; Singleton et al. 2006). As noted above, the modern spring and summer–fall run fish likely originated from the Methow and the Okanogan river basins (Fig. 1). Based on the available ^{87}Sr:^{86}Sr data, the bedrock geology of these basins may be further divided into three regions: the Methow; the Western Okanogan, including the Similkameen River; and the Eastern Okanogan. The Methow Basin includes igneous rock units of Jurassic–Cretaceous age, which typically have ^{87}Sr:^{86}Sr = 0.7029 to 0.7052 (Greig et al. 1992; Smith and Thorkelson 2002). The Western Okanogan region has igneous rocks similar to those found in the Methow Basin but also has rocks with ^{87}Sr:^{86}Sr values from 0.7046 to 0.7093 and minor rock units with values as high as 0.7355 (Menzer 1970; Petö and Armstrong 1976). The Eastern Okanogan Basin includes rocks with relatively high ^{87}Sr:^{86}Sr values (~0.7199 to 0.7270) (Kyser et al. 1994; Hinchey and Carr 2006). In the southern part of the Okanogan Basin, ^{87}Sr:^{86}Sr

river values would also be influenced by rocks on the west side of the river with lower average values (~0.7065) (Dostal et al. 2003). The archaeological otoliths would have come from fish migrating up the Columbia River mainstem to the headwaters or possibly tributaries such as the San Poil, Spokane, or Pend Oreille rivers (Fig. 1).

To supplement the information on bedrock geology, we collected water samples from various river locations (Fig. 1*a*) for determination of $^{87}Sr/^{86}Sr$, Sr, and Ca. Samples were collected in acid-washed plastic bottles, chilled, filtered (0.25 μm) within 24 h, and acidified with high purity HNO_3. Riverine $^{87}Sr/^{86}Sr$ was determined using MC-ICP-MS at the University of Washington (Seattle, Washington); data were normalized relative to standard reference material NBS 987 (±25 ppm; 2 SE). Sr and Ca data were collected using a Teledyne Leeman Prodigy ICP-optical emission spectrometer. Standard calibrations were generated with standard reference material of known concentration (SPEX Certiprep Group). Samples of standard reference material NIST1643e were introduced throughout the run to estimate accuracy (±2%) and precision (±2%).

In anadromous salmonids, the region of the otolith that is formed prior to yolk-sac absorption can be enriched in marine Sr because vitellogenesis begins during maternal ocean residence (Kalish 1990; Miller and Kent 2009). To characterize only the natal source, otolith $^{87}Sr/^{86}Sr$ data must be collected outside of the maternally influenced region. Therefore, to generate an estimate of $^{87}Sr/^{86}Sr$ during initial river residence, we averaged $^{87}Sr/^{86}Sr$ data across a 40 μm portion of the otolith immediately outside of the maternally influenced region (Fig. 2). Freshwater otolith $^{87}Sr/^{86}Sr$ values were then grouped by similarity and compared using analysis of variance (ANOVA) on rank-transformed data to meet assumptions of normality and homogeneity of variance (Zar 1996). Statistically homogeneous groups were determined using the Tukey honestly significant difference (HSD) test. Statistica (version 9.1, StatSoft Inc., Tulsa, Oklahoma) was used for all analyses.

Natal otolith $^{87}Sr/^{86}Sr$ values will differ among and within sample groups if individuals originated in rivers with distinct $^{87}Sr/^{86}Sr$ values. However, given that all individuals inhabited marine waters with $^{87}Sr/^{86}Sr = 0.70918$ during the later portion of their life history, this portion of the otolith should display consistent and similar values. Therefore, we averaged $^{87}Sr/^{86}Sr$ data across a 40 μm portion near the outer edge of each otolith to generate a mean marine otolith $^{87}Sr/^{86}Sr$ (Figs. 2*b*, 2*d*). Differences in otolith $^{87}Sr/^{86}Sr$ during marine residence were compared among sample groups (i.e., modern spring run, modern summer–fall run, and archaeological) using ANOVA on rank-transformed data. This provided a quantitative assessment of marine otolith $^{87}Sr/^{86}Sr$; significant differences between modern and archaeological marine $^{87}Sr/^{86}Sr$ values would indicate postdepositional alteration.

Reconstruction of juvenile migratory history

Habitat transitions of individual fish, such as movement from riverine to brackish–oceanic waters, can be identified by variation in otolith composition when there is adequate chemical variation among the habitats of interest. For anadromous species, increases in otolith Sr:Ca can be used to identify individual movement into brackish–oceanic waters if freshwater Sr:Ca is lower than marine Sr:Ca (Secor et al. 1995; Kraus and Secor 2004; Miller et al. 2010*a*). Additionally, freshwater $^{87}Sr/^{86}Sr$ is often distinct from the global marine value (= 0.70918) (Palmer and Edmond 1989; Bacon et al. 2004). Therefore, variation in $^{87}Sr/^{86}Sr$ between freshwater and marine systems can also be used to identify diadromous movements (Kennedy et al. 2002; Bacon et al. 2004).

We used Sr:Ca and $^{87}Sr/^{86}Sr$ values obtained along transects of the modern and archaeological otoliths to estimate when juveniles emigrated from fresh water. We identified the time of freshwater emigration (i.e., initial entrance into brackish waters) by the inflection points on the life history profiles of Sr:Ca and (or) $^{87}Sr/^{86}Sr$ prior to stabilizing at marine values (Figs. 2*a*–2*d*). We then measured otolith width (OW, μm) at this transition and used a previously developed relationship between OW and fork length (FL, mm) to estimate juvenile size at freshwater emigration (Miller et al. 2010*a*). All OWs were measured with Image Pro Plus (Media Cybernetics, Bethesda, Maryland). Fish were classified as yearling or subyearling based on size at freshwater emigration and the location of the first winter annulus (i.e., before or after freshwater emigration, respectively). Differences in size at freshwater emigration among the four groups of Chinook salmon were compared with ANOVA on rank-transformed data.

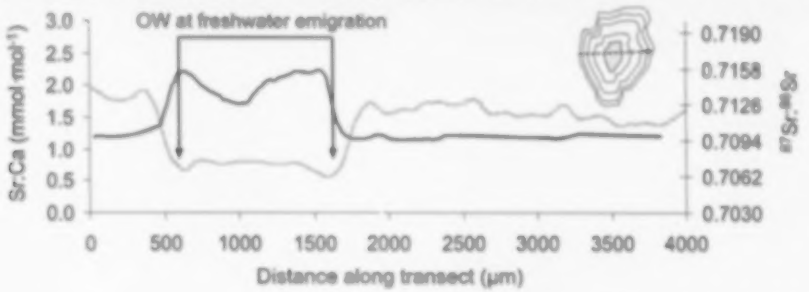
Estimation of adult body size upon return to the Columbia River

We completed a linear regression analysis of adult FL (cm) and otolith length (OL, mm) along the anterior–posterior growth axis for the modern adult otolith samples and used the relationship to estimate adult size (FL) upon return to the Columbia River for the archaeological samples. For the adult stage, OL is a better predictor of FL than OW. All OLs were measured with Image Pro Plus (Media Cybernetics). Differences in observed FL of the modern runs and estimated FL of the archaeological samples were compared with ANOVA on rank-transformed data.

Related assessment of otoliths

Initial inspection of archaeological otoliths indicated varying levels of breakage, surface erosion, and surface accretion (i.e., irregular growth on surface). Given that fracturing can accelerate chemical alteration (Banner 1995), breakage and (or) visual expression of surface alteration may be an indicator of postdepositional alteration. Therefore, we developed a ranking criteria (Behrensmeyer 1978) to quantify visual damage based on digital images of the distal surface of whole otoliths: 0–1: no visual damage, similar to modern otolith; 1–2: one break or light surface erosion or accretion; 2–3: two breaks or heavy surface erosion or accretion; 3–4: more than two breaks or heavy erosion and (or) accretion; 4–5: more than two breaks and heavy erosion and accretion. Otoliths were ranked independently by two of the authors and a mean rank was calculated. We determined if mean rank was correlated with observed marine otolith $^{87}Sr/^{86}Sr$. We used the marine $^{87}Sr/^{86}Sr$ because unlike the natal otolith $^{87}Sr/^{86}Sr$, the values are expected to be similar among all samples. One specimen (Archaeo 3) was excluded from the ranking because we did not have a whole otolith image. We also used scanning electron microscopy (Tescan Vega-II

Fig. 3. Sr:Ca (mmol·mol^{-1}) (gray line) and ^{87}Sr:^{86}Sr (black line) across the ventral–dorsal growth axis of an archaeological Chinook salmon otolith. Measurements of otolith width (OW, μm) at freshwater emigration are identified.



SBH) to acquire images of the daily increments in a modern and archaeological otolith for visual comparison.

Results

Otolith Sr:Ca and ^{87}Sr:^{86}Sr

Sr:Ca across the growth axis of modern otoliths demonstrated the expected pattern of low Sr:Ca (<1.2 mmol·mol^{-1}) during presumed freshwater residence and higher values during marine residence (1.4 to 2.5 mmol·mol^{-1}) (Figs. 2*b*, 2*d*). Sr:Ca across the growth axis in the archaeological otoliths also met general expectations: Sr:Ca ratios were <0.9 mmol·mol^{-1} during presumed freshwater residence, and marine values ranged from 1.5 to 2.2 mmol·mol^{-1} (e.g., Fig. 3).

^{87}Sr:^{86}Sr across the growth axis of modern otoliths also demonstrated the expected pattern of variable freshwater and consistent marine values of 0.70918 (Fig. 2). Although transects of all archaeological otoliths displayed the expected general patterns of initial freshwater and then ocean residence (Fig. 3), the ^{87}Sr:^{86}Sr data indicated that the archaeological otoliths were affected by some diagenesis. In particular, ^{87}Sr:^{86}Sr values at the edges of the archaeological otoliths, which represent oceanic residence, were higher than the modern spring and summer–fall otoliths ($F_{[2,28]} = 22.8$, $p < 0.001$, Tukey's HSD $p < 0.05$). Seven of the modern fish were not included in this statistical analysis because ^{87}Sr:^{86}Sr data were not collected at the outermost edge of their otoliths. The range in otolith ^{87}Sr:^{86}Sr during presumed ocean residence for the archaeological samples was 0.70927–0.70960 (Fig. 4*a*), which represents a shift to more radiogenic values of 90–420 ppm.

Natal sources

The riverine ^{87}Sr:^{86}Sr values confirmed our expectations based on bedrock geology and provided additional spatial resolution (Table 1, see Fig. 1*a* for locations). For example, the Okanogan River Basin displays a range of bedrock ^{87}Sr:^{86}Sr values (0.7046–0.7270), yet the mainstem Okanogan River above the influence of the mainstem reservoir below Chief Joseph Dam (i.e., Lake Pateros) displays a moderate to low ^{87}Sr:^{86}Sr value of 0.70584. Within the reservoir, the water values (0.71528) are clearly influenced by the mid-Columbia mainstem waters (0.714–0.715). Similarly, as expected, the highest water ^{87}Sr:^{86}Sr values were observed within the most eastern portion of the basin, above Grand Coulee Dam (0.71727).

Otolith ^{87}Sr:^{86}Sr values during initial freshwater residence indicate that there were four distinct natal sources for the modern Chinook salmon and at least four sources for the archaeological specimens (Fig. 4*c*). For the modern spring run, all but one individual displayed a consistent pattern of low freshwater ^{87}Sr:^{86}Sr, indicative of residence in similar, if not the same, river systems (mean ± 2 SE = 0.70438 ± 0.00096, $n = 14$) (Fig. 4*c*). One spring run individual was distinct (mean otolith ^{87}Sr:^{86}Sr = 0.70683). All the values except one are similar to the riverine ^{87}Sr:^{86}Sr values for the Methow Basin (~0.7043). The summer–fall run samples displayed two dominant provenance patterns: mean otolith ^{87}Sr:^{86}Sr ± 2 SE = 0.70651 ± 0.00021 ($n = 8$) and 0.71140 ± 0.00020 ($n = 10$) (Fig. 4*c*). One individual had a mean otolith ^{87}Sr:^{86}Sr = 0.71451. Based on bedrock and riverine ^{87}Sr:^{86}Sr values, it is plausible that the summer–fall run individuals with ^{87}Sr:^{86}Sr = 0.70651 originated in the Okanogan River. Given ^{87}Sr:^{86}Sr values in the mid-Columbia River region (0.714–0.715) (Table 1), the distinctive summer–fall individual may be the progeny of a mainstem spawner. However, it is unlikely that the individuals with ^{87}Sr:^{86}Sr = 0.71140 originated within the Okanogan River. Therefore, with the exception of the one summer–fall individual (^{87}Sr:^{86}Sr = 0.71451), the remaining modern samples were visually grouped by natal otolith ^{87}Sr:^{86}Sr, and mean differences among those three groups were statistically significant ($F_{[2,30]} = 121.6$, $p < 0.001$, Tukey's HSD $p < 0.05$) (Fig. 4*b*).

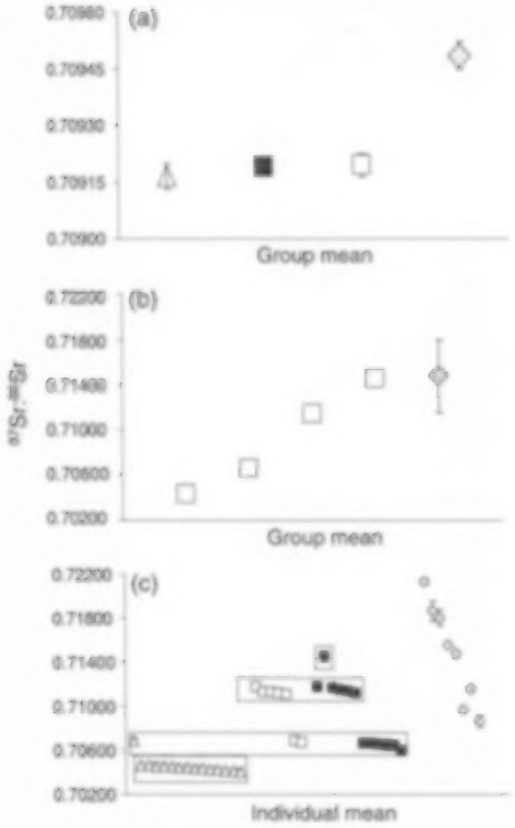
Natal ^{87}Sr:^{86}Sr values of the archaeological otoliths ranged from 0.70966 to 0.72134 (Fig. 4*c*). Given the observed shift (90–420 ppm) in the marine ^{87}Sr:^{86}Sr values of the archaeological otoliths, it is likely that the natal ^{87}Sr:^{86}Sr values also shifted since deposition. Therefore, natal ^{87}Sr:^{86}Sr values of archaeological and modern otoliths were not compared in a quantitative manner. Despite the observed diagenesis, it appears that none of the archaeological samples originated in low ^{87}Sr:^{86}Sr watersheds similar to the modern spring run Chinook salmon (Fig. 4*c*). Additionally, three of the archaeological otoliths displayed substantially more radiogenic ^{87}Sr:^{86}Sr values (>0.7180) than observed in any of the modern otoliths.

Reconstruction of juvenile migratory history

We used eq. 1 to estimate juvenile size at freshwater emigration (Miller et al. 2010*a*).

(1) $\quad FL = 0.060\ (\pm 0.002\ SE) \times OW + 6.91\ (\pm 2.19\ SE)$

Fig. 4. Otolith ^{87}Sr:^{86}Sr for modern and archaeological Chinook salmon. (*a*) Otolith ^{87}Sr:^{86}Sr (mean ± 2 standard errors, SE) during residence in oceanic waters for modern spring run Chinook salmon (triangles: $n = 9$), modern summer–fall run yearlings (filled squares: $n = 2$), modern summer–fall subyearlings (open squares: $n = 8$), and archaeological otoliths (filled diamonds: $n = 8$). (*b*) Mean (±2 SE) otolith ^{87}Sr:^{86}Sr during initial freshwater residence for statistically homogeneous groups for modern samples (open squares) along with the mean (±2 SE) for the archaeological collections (filled diamond). (*c*) Otolith ^{87}Sr:^{86}Sr during initial freshwater residence for Chinook salmon for modern and archaeological collections (individual mean ± 2 SE). Open triangles indicate modern spring run Chinook salmon; open squares indicate modern summer–fall run, yearlings; filled squares indicate modern summer–fall subyearlings; and gray diamonds indicate archaeological otoliths. Boxes denote individuals within each of the statistically distinct groups presented in (*b*).



For juveniles >175 mm FL, eq. 1 underestimates FL. As the majority of Columbia River Chinook salmon (>90%) enter brackish waters at sizes <175 mm FL (Rich 1920; Giorgi et al. 1994; Tiffan et al. 2000), we used this relationship to estimate juvenile size at the time of freshwater emigration to brackish–ocean waters.

Based on these estimates, modern yearling individuals were the largest upon freshwater emigration ($F_{[3,38]} = 23.7$, $n = 42$, $p < 0.001$, Tukey's HSD $p < 0.05$). However, there was no difference between yearlings from the spring and summer–fall runs (Tukey's HSD $p > 0.10$). The mean calculated size at freshwater emigration for the archaeological samples was statistically similar, although slightly smaller, than the modern subyearlings (Fig. 5*a*). Our otolith-derived estimates for size at freshwater emigration for modern spring and summer–fall run individuals fall within the observed size range for middle and upper Columbia spring and summer–fall run juveniles collected in recent (2002–2007) beach and purse seines in the estuary (Fig. 6; D. Bottom, National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center (NOAA NWFSC), Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington, unpublished data).

Estimation of adult size body upon return to the Columbia River

For modern adults, FL (cm) was linearly and positively related with OL for fish that were <95 cm FL with OL <14 mm ($r^2 = 0.85$, $n = 22$, $p < 0.001$):

$$(2) \quad FL = 9.2\ (\pm 0.9\ SE) \times OL - 24.3\ (\pm 10.2\ SE)$$

For otoliths ≥14 mm, OL underestimated adult FL. Eight modern individuals were excluded from this analysis because they had broken otoliths ($n = 6$) or were classified as immature ($n = 2$) based on their reproductive state. Because all archaeological otoliths were <14 mm, we used eq. 2 to estimate adult body size of these samples (Appendix A, Table A1).

For modern runs, observed adult size (FL) ranged from 64 to 112 cm. Adult size ranged from 73 to 95 cm FL for spring run yearlings; 81 to 112 cm FL for summer–fall run yearlings; and 64 to 101 cm FL for summer–fall run subyearlings. Based on eq. 2, the estimated adult body size of the archaeological samples ranged from 67 to 94 cm FL. Mean adult body size was significantly different among the four groups ($F_{[3,38]} = 3.7$, $n = 40$, $p = 0.02$). The estimated mean adult size of the archaeological samples was significantly smaller than the summer–fall run yearlings but similar to both the modern summer–fall run subyearlings and spring run yearlings (Fig. 5*b*).

Related assessments of otoliths

The mean rank of visual damage was positively and significantly correlated with observed marine ^{87}Sr:^{86}Sr otolith values (Pearson's $r = 0.77$, $n = 7$, $p < 0.05$; Figs. 7*a*–7*d*). All of the archaeological otoliths were collected from the same layer and date to the same period (250–500 years ago); thus, we have no independent basis for determining whether the observed variation in marine ^{87}Sr:^{86}Sr among samples is related to length of time since deposition. However, we note that the variation in marine ^{87}Sr:^{86}Sr among archaeological otoliths was not correlated with otolith size (i.e., length, width, or total area) (Pearson's $r < 0.30$, $n = 7$, $p > 0.50$). Fine-scale increment structure was visible in an archaeological otolith and appeared similar to a modern specimen (Figs. 7*e*–7*f*).

Discussion

The information extracted from the admittedly small sample size of archaeological Chinook salmon otoliths collected

Table 1. Riverine $^{87}Sr/^{86}Sr$, Sr (ppb), and Sr:Ca (mmol·mol^{-1}) data for various locations in the Columbia River Basin.

ID	Location	Riverine $^{87}Sr/^{86}Sr$	Sr (ppb)	Sr:Ca (mmol·mol^{-1})	Source
A	Columbia River mainstem, below Bonneville Dam	0.713278	66.0	2.35	This study
B	Columbia River mainstem, below Dalles Dam	0.713042	62.6	2.32	This study
C	Columbia River mainstem, below John Day Dam	0.713906	73.0	2.36	This study
D	Columbia River mainstem, below McNary Dam	0.713570	66.9	2.30	This study
E	Columbia River mainstem, above Priest Rapids Dam	0.71400	81.5	—	Singleton et al. 2006
F	Columbia River mainstem, ~12 RK downstream of Chief Joseph Dam	0.715283	76.6	2.07	This study
G	Columbia River mainstem, below Chief Joseph Dam	0.716671	72.4	1.94	This study
H	Columbia River mainstem, below Grand Coulee Dam	0.716661	73.0	1.95	This study
J	Columbia River mainstem, above Grand Coulee Dam	0.717270	67.3	1.93	This study
K	Columbia River mainstem, below Pend Oreille River	0.71563	74.0	1.78	Wadleigh et al. 1985
L	Snake River, above confluence with Columbia River	0.710339	53.3	3.06	This study
M	Yakima River	0.70731	136.0	—	Singleton et al. 2006
N	Methow River, approximately RK 35	0.704275	83.7	3.23	This study
O	Twisp River, tributary to the Methow River	0.704374	55.7	2.58	This study
P	Okanogan River, at approximately RK 25	0.705838	128.4	3.26	This study

Note: Samples below mainstem dams were collected within 5 km of the dam unless otherwise noted. Sample sites are identified by letters; see Fig. 1 for approximate locations. RK, river kilometre; —, no data.

in the upper Columbia River Basin provides novel insights on the life history of extirpated salmon populations that is germane to contemporary salmon conservation and recovery. The combined evidence indicates that the life history of the fish represented by these archaeological specimens was most similar to the modern summer–fall subyearling run. We tentatively suggest that these individuals would be included in the modern definition of the upper Columbia summer–fall run ESU. As currently defined, the upper Columbia summer–fall run ESU is composed of fish that spawn in areas between McNary Dam (45°55′N, 119°17′W), which is located 470 km from the mouth of the Columbia River, and Chief Joseph Dam (Myers et al. 1998). Fish from this ESU primarily display a subyearling life history, and substantial differences in life history and genetics distinguish fish in this ESU from the middle and upper Columbia River spring run ESUs.

Prior to major hydropower development, Chinook salmon migrated some distance upstream of the current location of Grand Coulee Dam to spawn. According to Fulton (1968), individuals from the summer run migrated further upriver than those from the fall run, and there are reports of large, summer run Chinook salmon passing the natural obstruction at Kettle Falls and arriving at Windermere Lake, British Columbia, at the headwaters of the Columbia River (Bryant and Parkhurst 1950). Our data provide further evidence for a predevelopment subyearling life history above Chief Joseph Dam, the current upstream extent of salmon distribution. The individuals we examined could have originated within the mainstem Columbia River anywhere above Chief Joseph Dam or within the Spokane or Pend Oreille rivers. However, origination in the San Poil Basin is unlikely for all except two of the archaeological samples because of low values of bedrock and riverine $^{87}Sr/^{86}Sr$ (<0.7096) (Morris et al. 2000). The high $^{87}Sr/^{86}Sr$ values (>0.718) observed in three of the archaeological otoliths indicate that these fish originated relatively high in the basin where more radiogenic waters may occur. Potential sources include the mainstem of the Columbia River upstream of the Pend Oreille River or within the Pend Oreille or Spokane rivers. However, there was a major waterfall on the Spokane River, ~80 km upriver of its confluence with the Columbia River, which was a likely barrier (Fulton 1968).

We were interested in determining if the level of diagenesis would limit our ability to examine other samples from different locations or time periods. Chinook salmon otoliths are composed of aragonite, which is considered more prone to diagenesis than other polymorphs of calcium, such as calcite (Marshall 1992). Diagenesis can occur because of cementation, recrystallization, or replacement, and the rate of alteration depends on the local burial conditions and sample porosity, among other factors (Banner 1995; Cuif et al. 2008). Although fracturing alone does not usually lead to chemical alteration, it may aid the passage of fluids and allow, or accelerate, subsequent alteration (Banner 1995). Depending on the method of chemical alteration and the element or isotope under consideration, the pattern of diagenesis can result in a linear covariance between the original and local source, which would allow for correction via "backstripping" (i.e., extrapolation) if original values are known (Marshall 1992). In this study, all archaeological otoliths displayed similar directionality in their shift to more radiogenic $^{87}Sr/^{86}Sr$ marine values. Given that marine $^{87}Sr/^{86}Sr$ is increasing at a very slow rate (Hess et al. 1986), the increase in otolith $^{87}Sr/^{86}Sr$ values cannot be due to changes in the ocean values. Water $^{87}Sr/^{86}Sr$ values in the mainstem Columbia River in the vicinity of the archaeological site were ~0.7167; therefore, local substitution should result in more radiogenic values as was observed. Furthermore, if substitution was occurring in a linear manner and the diagenetic Sr is similar to surface waters at the archaeological site, the overall substitution ranged from 3% to 16% within 250–500 years. If Sr diagenesis occurs at a constant rate, we would expect 32%–65% Sr substitution in 1000-year-old samples. One option for future analyses is to use the observed shift from expected marine $^{87}Sr/^{86}Sr$ values during ocean residence, in conjunction with data on $^{87}Sr/^{86}Sr$ values at the burial environment, to estimate the extent of local substitution and correct (or backstrip) the observed natal otolith

Fig. 5. Mean (±2 standard errors, SE) size of modern and archaeological Chinook salmon. (*a*) Estimated juvenile fork length (FL, mm) at freshwater emigration. Data are included for modern spring run yearlings, modern summer–fall (Su–Fall) run yearlings and subyearlings, and for archaeological samples. Statistically similar groups are denoted by the same letter. (*b*) Adult body size (FL, cm) for modern and archaeological specimens. For modern runs, body size was measured in the field, and for archaeological samples, body size was estimated using the observed relationship between body size and otolith length for modern runs.

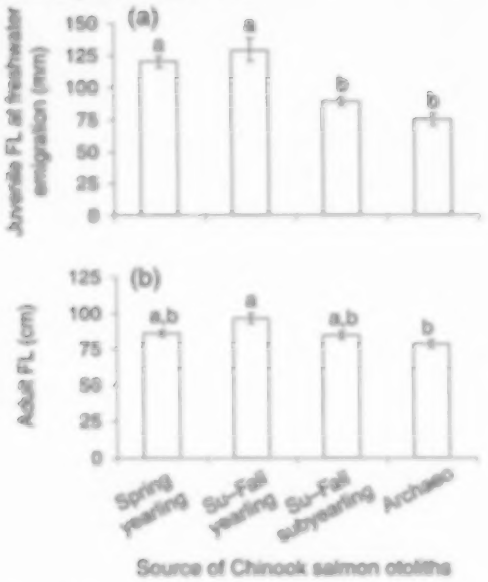
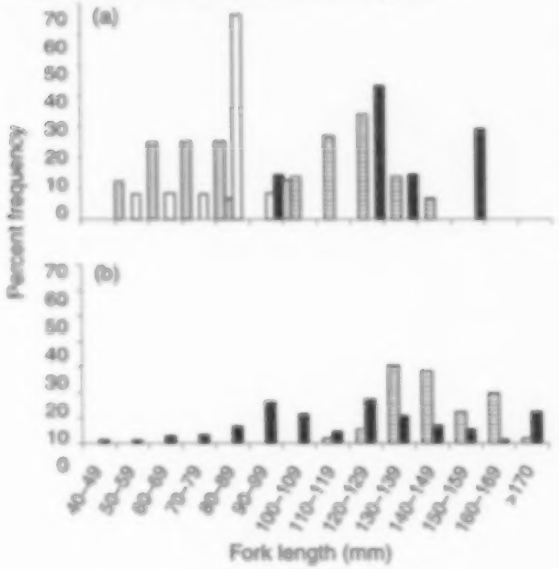


Fig. 6. Size frequency of juvenile Chinook salmon from the mid- and upper Columbia River. (*a*) Back-calculated size at freshwater emigration (fork length (FL), mm) for modern and archaeological Chinook salmon based on adult otolith analysis. Open bars indicate modern spring run Chinook salmon (n = 15); hatched bars indicate modern summer–fall run yearlings (n = 7); filled bars indicate modern summer–fall subyearlings (n = 12); and gray bars indicate archaeological otoliths (n = 12). (*b*) Size (FL, mm) of modern middle and upper Columbia River spring and summer–fall run Chinook salmon from estuarine beach and purse seines collections (2002–2007). Hatched bars represent modern spring run (n = 56), and filled bars represent modern summer–fall run (n = 76). Unpublished data for (*b*) provided by D. Bottom, NOAA NWFSC, Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington.

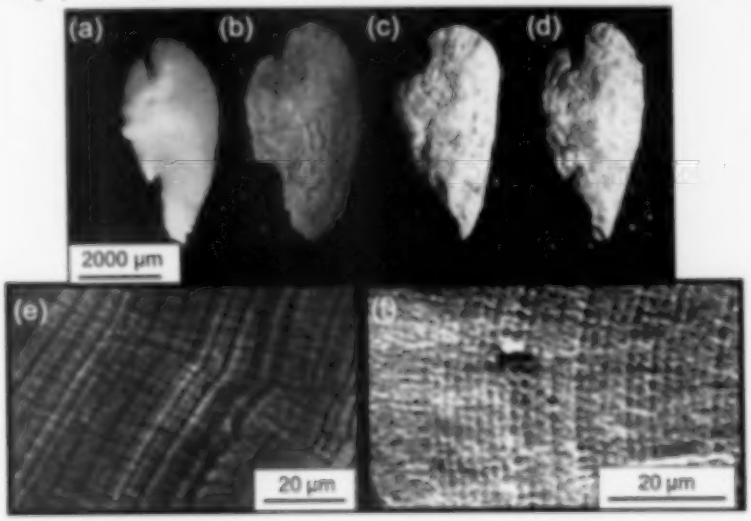


^{87}Sr:^{86}Sr values (Marshall 1992). Alternatively, samples older than ~500 years could receive additional sample treatment, such as acid leaches, to remove diagenetic strontium (Dufour et al. 2007). In situations where adequate numbers of samples are available, those with the least extent of visible surface alteration could be included preferentially. Other analysis, such as X-ray diffraction, could also provide information on whether observed shifts in marine ^{87}Sr:^{86}Sr of archaeological samples are correlated with replacement of aragonite by another mineral form (e.g., apatite or calcite; Stathopoulou et al. 2008; Kasioptas et al. 2010).

A related point on the ability to determine provenance in extant populations is highlighted by the lack of correspondence between regional and otolith ^{87}Sr:^{86}Sr in eight of the modern samples. Based on natal otolith ^{87}Sr:^{86}Sr, it is highly unlikely that eight of the modern summer–fall run fish originated within the Okanogan River or the Columbia River mainstem upstream of Wells Dam. The Eastbank Hatchery, located on the Columbia River adjacent to Rocky Reach Dam, produces summer run Chinook salmon that are transferred to the Similkameen Acclimation Pond on the Okanogan River for 2 weeks prior to release. Because otolith ^{87}Sr:^{86}Sr can be influenced by food, otolith ^{87}Sr:^{86}Sr in hatchery fish is often shifted toward marine ^{87}Sr:^{86}Sr values because of the use of feed dominated by marine protein (^{87}Sr:^{86}Sr = 0.70918) (22%–42% food contribution; Miller et al. 2010*b*). Therefore, given mainstem river ^{87}Sr:^{86}Sr (0.714–0.715), it is most likely that the fish with natal ^{87}Sr:^{86}Sr = 0.71140 originated from the Eastbank Hatchery and were transferred to the Okanogan River as juveniles. This conclusion is supported by a recent study characterizing natal otolith ^{87}Sr:^{86}Sr values in several Columbia River hatcheries; Barnett-Johnson et al. (2010) reported natal otolith ^{87}Sr:^{86}Sr of 0.71113 ± 0.00023 (mean ± 1 SD; n = 10) for Eastbank Hatchery summer Chinook salmon, values very similar to the eight otoliths in this study. The accuracy of scale analysis to differentiate hatchery and naturally produced fish could be further evaluated through examination of natal otolith ^{87}Sr:^{86}Sr in additional samples.

Waples et al. (2008) note the potential for evolutionary change in salmonid life history traits as a result of the Columbia River hydropower system, which has reduced average and peak stream flows, increased residence times of water, and altered water temperatures. Given that at least a component of juvenile migratory timing is heritable (Taylor 1991), alteration of the selective environment can lead to changes in migration timing (Waples et al. 2009); this is exemplified by the recent development of a reservoir-type life history within the predominantly subyearling Snake River fall run Chinook salmon population (Connor et al. 2005; Williams et al.

Fig. 7. Images of modern and archaeological otoliths. Distal surface of whole (*a*) modern and archaeological otoliths (*b*–*d*). Archaeological samples are arranged along a gradient of $^{87}Sr:^{86}Sr$ ratios observed at the otolith edge (i.e., during presumed ocean residence). Marine $^{87}Sr:^{86}Sr$ values are as follows: (*a*) 0.70919; (*b*) 0.709267; (*c*) 0.709495; (*d*) 0.70953. Note that the visible extent of surface erosion increases from (*b*) to (*d*). Scanning electron micrographs of daily increments in (*e*) modern and (*f*) archaeological otolith are also shown.



2008). Currently, the peak arrival time of upriver juveniles in the estuary occurs approximately 2 weeks later than historical accounts (Park 1969; Bottom et al. 2005). Although we cannot independently determine arrival time of the fish represented by our archaeological samples, we note that their comparatively small sizes (59–101 mm FL) point to a relatively early arrival.

Rich (1920) observed juvenile Chinook salmon 40–100 mm FL in the Columbia River estuary during June and July, which is similar to the estimated size at freshwater emigration for the archaeological samples (59–101 mm FL). Park (1969) noted that prior to the impoundments on the upper Columbia River, most juveniles from the summer runs emigrated in their first year of life. He further commented that "there was no significant downstream migration of juvenile Chinooks after June" at Bonneville Dam from 1946 to 1953 (Park 1969). Recent work indicates that upper Columbia summer–fall run Chinook salmon juveniles 40–173 mm FL comprised approximately 6% of the beach seine collections in the Columbia River estuary (D. Bottom, NOAA NWFSC, Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington, unpublished data). In that study, 61% of the upper Columbia River summer–fall juveniles fell within the size range of our archaeological samples (59–101 mm FL) and were mostly captured in June and July sampling (D. Teel, NOAA NWFSC, Manchester, Washington, personal communication, 2009). Thus, it appears that the size at and approximate timing of juvenile migration observed in the archaeological samples is similar to a component of the extant upper Columbia summer–fall run.

We found no evidence of yearling emigrants in our archaeological samples. Although some information indicates that prior to the impoundments on the upper Columbia River, most juveniles from summer runs emigrated in their first year of life (Park 1969), Myers et al.'s (1998) synthesis indicates that 12%–42% of the summer run populations in the upper Columbia River emigrated as yearlings. More archaeological samples are needed to draw any conclusions regarding the extent of variation in predevelopment life histories. Furthermore, if the indigenous fishery occurred mainly during late summer during low flow periods, the archaeological otoliths would represent a biased sample of the predevelopment Chinook salmon life histories. Although it is not clear how important yearling emigrants were to upper Columbia River Chinook salmon populations, there has been an increase in the number and proportion of summer–fall Chinook salmon released from upper Columbia River hatcheries as yearlings. In the early 1970s, less than 2 million summer–fall run Chinook salmon were released from hatcheries and none of these were yearlings. In the last 5 years, approximately 2–5 million fish were released annually and 26–56% of those were released as yearlings (Regional Mark Processing Center: http://www.rmpc.org/).

We have demonstrated the feasibility of reconstructing aspects of the life history of an anadromous species based on 250- to 500-year-old otoliths. With adequate background information, similar approaches would be applicable to other anadromous species. Information on life history variation prior to development provides a baseline with which to assess the status of extant populations. The combined evidence indicates that the extirpated population reflected in the archaeological otoliths represents a summer–fall run with a subyearling life history. The presence of similar life history traits in some of the extant samples suggests that this Chinook salmon life history pattern persists in the Columbia River system. As Healey (2009) notes, management strategies may promote the dominant tactic, or phenotype, thereby reducing life history variation, which may in turn reduce population resiliency. Alternatively, as exemplified by the recent development of the reservoir-rearing life history (Connor et al. 2005; Williams et al. 2008), changes in the selection environment can also promote novel phenotypes. The

relative importance of genetic vs. environmental factors in the development and maintenance of juvenile migratory history remains uncertain. However, a reduction in life history diversity in Chinook salmon has occurred since the development of the Columbia River Basin, at least partially because of the great reduction in historic spawning habitat, changes in hydrology, and the establishment of an extensive hatchery program (Bottom et al. 2005). It appears that the potential to maintain aspects of the predevelopment life history variation within the modified landscape of the Columbia River still exists, and further action to implement management strategies that promote maintenance of that life history diversity is warranted.

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Appendix A

Table A1 follows on next page.

Table A1. Life history characteristics of individual Chinook salmon based on archaeological (estimated) and modern (observed) otolith collections.

ID	OL (cm)	Adult FL (cm)	OW at freshwater emigration (μm)	Size at freshwater emigration (FL, mm)
Archaeological				
Archaeo 1	11.2	79	890	60.3
Archaeo 2	10.0	68	861	58.6
Archaeo 3	11.5	82	965	64.8
Archaeo 4	11.3	79	1128	74.6
Archaeo 5	11.1	78	1128	74.6
Archaeo 6	11.5	82	1217	79.9
Archaeo 7	12.9	94	1252	82.0
Archaeo 8	9.9	67	1571	101.2
Modern				
Sp yearling 1	NA	94	1272	83.2
Sp yearling 2	13.6	90	1548	99.8
Sp yearling 3	NA	92	1750	111.9
Sp yearling 4	13.6	95	1657	106.3
Sp yearling 5	NA	73	1800	114.9
Sp yearling 6	12.7	87	1800	114.9
Sp yearling 7	14.0	89	1865	118.8
Sp yearling 8	13.0	90	1968	125.0
Sp yearling 9	14.0	90	1886	120.1
Sp yearling 10	NA	93	2016	127.9
Sp yearling 11	NA	76	2016	127.9
Sp yearling 12	8.2	48*	2001	127.0
Sp yearling 13	NA	74	2112	133.6
Sp yearling 14	11.5	75	2184	138.0
Sp yearling 15	14.0	88	2307	145.3
Su–Fa subyearling 1	11	94	953	64.1
Su–Fa subyearling 2	13.5	77	1152	76.0
Su–Fa subyearling 3	11.5	80	1410	91.5
Su–Fa subyearling 4	9.1	55*	1425	92.4
Su–Fa subyearling 5	9.6	64	1410	91.5
Su–Fa subyearling 6	12.1	97	1460	94.5
Su–Fa subyearling 7	10	65	1499	96.9
Su–Fa subyearling 8	12.2	101	1440	93.3
Su–Fa subyearling 9	12.2	94	1547	99.7
Su–Fa subyearling 10	NA	96	1368	89.0
Su–Fa subyearling 11	10.4	68	1392	90.4
Su–Fa subyearling 12	10.5	94	1416	91.9
Su–Fa yearling 1	11.5	81	1380	89.7
Su–Fa yearling 2	13.3	100	1894	120.6
Su–Fa yearling 3	13.0	97	1896	120.7
Su–Fa yearling 4	NA	112	1944	123.6
Su–Fa yearling 5	13.3	99	2058	130.4
Su–Fa yearling 6	13.1	91	2480	155.7
Su–Fa yearling 7	12.9	94	2530	158.7

Note: Adult fork length (FL, cm), otolith width (OW, μm) and length (OL, cm), and estimated size at freshwater emigration (FL, mm) are included. Sp = spring run, Su–Fa = summer–fall run. NA indicates otolith length could not be accurately measured because of breakage.

*Immature.

Environmental and fishing limitations to the rebuilding of the northern Gulf of St. Lawrence cod stock (*Gadus morhua*)

Yvan Lambert

Abstract: Time series of life history traits determining the reproductive potential and productivity of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence (nGSL) were obtained for the period covering the collapse and failure of the stock to recover. Decreasing trends in these traits were observed under unfavourable oceanographic conditions, with lowest values reached in the early 1990s. These changes had a negative impact on reproductive rate and instantaneous rate (r) of population growth. Estimates of r used as a proxy of stock productivity were negative when the stock collapsed, indicating that the biomass would have decreased even without fishing. Population abundance projections for the recent period suggest a potential increase in population size of 7.3% per year, with a doubling time of 10.5 years in the absence of exploitation and a near 0% rate with current fishing mortality, indicating that present harvesting does not allow any rebuilding of the stock. Given the similarities in environmental conditions and key life history traits, the situation in the nGSL might reflect the state of many northwest Atlantic cod stocks.

Résumé : Des séries temporelles des caractéristiques démographiques déterminant le potentiel reproducteur et la productivité de la morue franche (*Gadus morhua*) dans le nord du golfe du Saint-Laurent (nGSL) ont été obtenues pour la période couvrant l'effondrement et l'absence de rétablissement du stock. Des diminutions des valeurs de ces caractéristiques ont été observées sous des conditions océanographiques défavorables avec des minimums atteints au début des années 1990. Ces changements ont eu un impact négatif sur le taux de reproduction et le taux instantané d'accroissement de la population (r). Les estimés de r utilisé comme variable de remplacement de la productivité du stock étaient négatifs lorsque le stock s'est effondré indiquant qu'une diminution de la biomasse aurait été observée même en absence de pêche. Des projections d'abondance de la population pour la période récente suggèrent un potentiel d'accroissement de la taille de la population de 7,3 % par année avec un temps de doublement de celle-ci de 10,5 ans en absence d'exploitation et un taux pratiquement égal à 0 % sous le niveau actuel de mortalité par la pêche indiquant que la récolte actuelle ne permet aucune reconstruction du stock. En raison des similarités dans les conditions environnementales et les caractéristiques clés du cycle biologique, la situation observée dans le nGSL pourrait refléter l'état de plusieurs stocks de morue de l'Atlantique nord-ouest.

Introduction

Despite the moratorium on most of the northwest Atlantic cod (*Gadus morhua*) stocks that collapsed in the 1992–1994 period, few signs of recovery were observed for most of them (Shelton et al. 2006). This lack of recovery was attributed to a lower productivity mainly associated with increased natural mortality, decreased body growth, reduced recruitment rates in some cases, and fishing mortality even though removals were limited (Sinclair 2001; Chouinard et al. 2005; Shelton et al. 2006).

High exploitation rate similar to the levels observed for most cod stocks over the northern portion of the range of distribution in the northwest Atlantic was observed for cod in the northern Gulf of St. Lawrence (Shelton et al. 2006). Following a period where catches peaked at levels between 80 000 and 106 000 t (1980 to 1986), the fishery was under moratorium from 1994 to 1996 (DFO 2009). It reopened in 1997, with catches increasing progressively from 3000 to 7000 t in 2002. The decrease in abundance indices during that period led to a 1-year moratorium in 2003. Since 2004, the landings increased from 3300 to 6200 t. The abundance indices are remaining at levels similar to those observed following the first moratorium, indicating the absence of any rebuilding of the stock.

Northern Gulf of St. Lawrence (nGSL) cod stock is considered one of the least productive cod stocks in the North Atlantic (Dutil and Brander 2003; Dutil et al. 2003*a*). The stock that lives in cold water is characterized by small sizes-at-age (i.e., low growth), lower average fish condition, and marked seasonal cycle in energy reserves that may be a prominent feature of cold water poorly productive stocks (Lambert and Dutil 1997*b*; Dutil et al. 2003*a*). Moreover, in the early 1990s nutritional status of cod declined in late

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Table 1. Sampling months and years available for the different research surveys conducted in the northern Gulf of St. Lawrence that were used to build the time series of the different life history traits of the cod stock between 1984 and 2008.

Life history traits	Sampling periods
Lengths-at-age	Jan. 1984–1994; July 1995–2001; May 2002; July 2003, 2004; May 2005–2008
Condition factor	Jan. 1984–1994; May 1994, 1995, 1997–2008; Jan. 2000–2007
Maturity	Jan. 1984–1994; May 1995, 1997, 1998, 2001, 2002, 2004–2008
Fecundity	May 1995, 1998, 2001, 2002, 2004–2006
Sex ratio	Jan. 1984–1994; Aug. 1991–2008
Numbers-at-age	Jan. 1984–1994; Aug. 1990–2008; July 1995–2008

summer and at the onset of winter, indicating a decrease in the energy reserves of the fish, which led to a very poor condition in the spring for the 1992–1994 period (Lambert and Dutil 1997*b*). This lower condition was also accompanied by a progressive decline in growth (Dutil et al. 1999).

These observations suggest that the productivity of the stock may change rapidly over time. Observed changes in key life history traits may represent phenotypic and (or) genetic response to the environment and (or) fishing pressure. However, the coherence between cod stock dynamics and the important negative temperature anomalies observed on a large scale in the Northwest Atlantic from the mid-1980s to the mid-1990s (Colbourne 2004; Drinkwater and Gilbert 2004) were interpreted as evidence suggesting that the environment, which is already considered as a cold environment for cod, had a stronger role in explaining the 1985–1992 declines in cod abundances than previously thought (Rothschild 2007). It was hypothesized that these changes dramatically decreased the reproductive and recruitment potential of cod in the nGSL, leading to a decreased productivity of the stock, which contributed to its collapse in 1994 (Dutil et al. 2003*a*).

The aim of the present study was to determine the reproductive potential of cod in the nGSL, its annual variation over time in relation to environmental conditions, and the impact of these changes on the recovery potential of the stock. It is hypothesized that the poor environmental conditions of the early 1990s reduced the innate reproductive potential of the stock to a level that made a major contribution to its collapse and that fishing pressure at the current level of reproductive potential is not allowing population growth. Time series of life history traits determining the reproductive potential of cod in the nGSL were assembled for the period covering the collapse and the failure of the stock to recover. Age, length, maturity, fecundity, stock egg production, and age-specific survival were used to obtain annual estimates of age-specific survival and reproductive rates. Demographic models were used to estimate instantaneous rate of population growth (r) and stock-rebuilding in relation to environmental conditions and fishing pressure.

Materials and methods

Biological characteristics of cod in the nGSL were collated from research surveys conducted by Fisheries and Oceans Canada (DFO) (Fréchet et al. 2009). Data on age, length, mass, sex, maturity, and fecundity were obtained from annual groundfish surveys, sentinel fisheries conducted with the fishing industry, and some supplementary research and sentinel fishery surveys. Time series of the demographic parameters necessary for the analysis of reproductive potential and instantaneous rate of population growth on an annual basis were available from 1984 onwards.

Length-at-age

The time series for mean length-at-age was built from length and age data obtained annually between 1984 and 2008 (Table 1). Lengths-at-age calculated from January and May samplings were considered as representing fish length at spawning since growth is minimal between January and May–June (major spawning period). Fish eat little or not at all during winter and condition factor is decreasing, meaning that fish must use their accumulated energy to meet their maintenance needs during that period (Lambert and Dutil 1997*b*; Dutil et al. 2003*b*). Length and age data available for the month of July only were corrected to estimate mean length-at-age during spawning using years where length and age data were available for both May and July (2002; 2005 to 2007).

For each survey, stratified sampling of cod by 3 cm length groups was used for age determinations. Mean length-at-age was calculated from age–length keys for each year weighted by population abundance at length (1 cm length groups), abundance being calculated by areal expansion of the stratified arithmetic mean catch-at-length per tow (Smith and Somerton 1981).

Statistical comparisons of mean lengths-at-age between years were done on an age basis using age and length data from January and May samplings only. Corrected data (July samples) used to build the time series were excluded from the statistical tests. As normality and homogeneity of variance assumptions could not be met, analyses of variance (ANOVAs) on rank data (Friedman's test) with Bonferroni correction for multiple comparisons were used (Conover and Iman 1981; Quinn and Keough 2002). The Bonferroni adjustment is often seen as too conservative, but it protects against over-claiming the number of significant differences between pairs of values.

Time series of lengths-at-age was built by fitting von Bertalanffy growth curves to mean lengths-at-age for each year. Lengths-at-age were determined by

$$L_t = L_\infty \left\{ 1 - e^{[-K(t-t_0)]} \right\}$$

where L_t and t are mean length-at-age and age, respectively, and L_∞, K, and t_0 are the parameters of the von Bertalanffy growth curve.

Condition factor

The condition factor (Fulton's) used as an indicator of the energetic condition of cod (Lambert and Dutil 1997*a*, 1997*b*) was determined for two specific periods of the year: at the beginning of overwintering (i.e., January) and during the prespawning period in May (Table 1). Condition factor was estimated from somatic mass in May and from total mass in January, as no data on gonad mass were available for January samples between 1984 and 1993. Comparisons of condition factors calculated with both total and somatic masses indicated slight differences on the order of only 0.02–0.03 (i.e., 2.2%–3.8% difference) between the two measures in January (Lambert and Dutil 1997*b*).

Within each year, two-way ANOVAs or nonparametric Friedman tests were used to compare condition factor in relation to sex and maturity stage. All fish were kept in the absence of differences between sexes and maturity groups. When significant differences were detected, Tukey–Kramer's tests were used for multiple comparisons. In these cases, only mature females and sex and maturity groups showing no differences with the condition factor of mature females were kept. Selected fish for each sampling period were used to estimate the condition factor of mature cod for each year and month. Number of fish per year and month used for the analysis varied between 114 and 697. Lower numbers of fish were kept for January 2000, 2002, and 2005 and for May 1999, 2000, and 2003 (60–103 fish).

Comparisons of condition factor values between years were done by 10 cm size classes to take into account size effect on the condition factor observed for some of the years. Nonparametric Kruskal–Wallis tests were used to compare condition factor for each size class.

Time series representing the condition factor of mature cod in May was prepared for the 1984 to 2008 period. For the years where no data were available in May, estimates of K were obtained from a regression between K in January and K in the following month of May. Time series of condition factor-at-age during the prespawning period was constructed using mean length-at-age and corresponding values of condition factor-at-size estimated for the month of May.

Sex ratio

The proportion of female-at-age was obtained from estimates of fish numbers at age by sex in the annual research surveys (Table 1). Total abundance of males and females by 3 cm length class was calculated by areal expansion of the stratified arithmetic mean catch at length per tow (Smith and Somerton 1981). Age–length keys were then used to estimate total abundance of males and females at age for each year.

Proportion of mature females

Maturity stages of cod in the different surveys were used to estimate the proportion of females that were mature-at-age (Table 1). Each fish was identified as immature, maturing, spawning, or spent following macroscopic criteria defined by Kjesbu et al. (1990) and Morrison (1990). Mature categories (maturing, spawning, or spent) were pooled so that each female was classified as immature (i.e., juvenile) or mature (i.e., adult). Individual length and maturity data were weighted by catches, and the proportion of females mature-at-length was estimated using a logistic equation (Trippel et al. 1997). Proportion of females mature-at-age was estimated from the mean length-at-age and the corresponding proportion of females that were mature-at-length. Proportion of females mature-at-age for missing years (1996, 1999, 2000, and 2003) was estimated by interpolation with new maturity ogives calculated by cohorts.

The maturity ogives were modeled by a generalized linear model with a binomial error and logit link function (Probit procedure; SAS Institute Inc. 1999). Size and age at 50% maturity with 95% fiducial limits were also obtained with this procedure. Data were tested for significant year effect using generalized linear models where the effect of length was first removed and year was considered as a class variable (GENMOD procedure; SAS Institute Inc. 1999).

Potential fecundity

The potential fecundity of cod in the nGSL was determined during the prespawning period for 7 years (Lambert and Dutil 2000; Lambert 2008) (Table 1). A standard volumetric method was used to determine the number of oocytes per gram of wet ovary in 1995 and 1998 (Lambert and Dutil 2000), and the autodiametric fecundity method (Thorsen and Kjesbu 2001) was used for the determination in the other years (Lambert 2008). Comparisons of slopes obtained with linear regressions on log-transformed data and adjusted means with analysis of covariance (ANCOVA) were used to compare potential fecundity between years (Sokal and Rohlf 1995).

The dependence of potential fecundity on length and condition factor was used to develop a generalized linear model for fecundity (Lambert and Dutil 2000; Lambert 2008). Potential fecundity (F, number of oocytes) was described as

$$F = e^{[-0.709+3.630\ln(L)+1.515\ln(K)]}$$

where L represents fork length and K is the prespawning condition factor (i.e., May). This fecundity model was used with time series of mean length and condition factor-at-age to estimate the potential fecundity-at-age for the 1984 to 2008 period.

Potential fecundity data for the years 2004 to 2006 were also used to validate the fecundity model. Potential fecundity–length relationship for each year was compared with predicted fecundities of the model using length and mean condition factor at length for the same year.

Reproductive potential

Annual total egg production (TEP_t) of the stock was used as an index of the stock reproductive potential. It was estimated as

$$TEP_t = \sum_{x=3}^{11} N_{x,t} R_{x,t} M_{x,t} F_{x,t}$$

where $N_{x,t}$ is the number of fish at age x in year t, $R_{x,t}$ is the proportion of females at age x in year t, $M_{x,t}$ is the proportion of females that are mature at age x in year t, and $F_{x,t}$ is the potential number of eggs produced by a female at age x in year t.

Numbers-at-age were obtained from the sequential population analysis (SPA) of cod in the nGSL (Fréchet et al. 2009).

The SPA based on catches at age from the commercial fishery provided population estimates per age for each year. The SPA was calibrated using four indices of abundance coming from sentinel fisheries and scientific surveys conducted by DFO. The ADAPT statistical framework (Gavaris 1988) was used for the calibration.

Reproductive rate and intrinsic rate of population increase

Life tables incorporating age-specific rates of survival and reproduction were used to estimate reproductive rate and instantaneous rate of population increase (Caswell 2001). The intrinsic rate of population increase (r, malthusian parameter) was obtained by solving the Euler–Lotka equation:

$$\sum_{x=\alpha}^{w} e^{-rx} l_x m_x = 1$$

where l_x is the probability of survival to age x, m_x is the number of female offspring produced at age x, α is the age at first maturity, and w is the maximum reproductive age. A maximum reproductive age of 20 years was used for the calculations.

Intrinsic rate of increase is defined as the maximum rate of population increase (Myers et al. 1999; McAllister et al. 2001; Gedamke et al. 2007). This maximum rate should occur in the absence of fishing at low population size when density-dependent effects are at a minimum. A stable age distribution is also assumed. In the presence of significant density effects and large deviation from a stable age distribution, estimates of r would be different than the true intrinsic rate of increase. As we may not assume that these conditions were always met, r in the present study was defined as the instantaneous rate of population growth that would be realized or achieved given the observed sets of life history parameters for the different years. Nevertheless, considering that the abundance level of cod in the nGSL since the beginning of the 1990s only represents 3.5% to 11% of the abundance levels observed in the 1980s (Fréchet et al. 2009), it can probably be assumed that density effects are at minimal levels.

Year-specific estimates of reproductive rate and instantaneous rate of population increase were calculated for the period between 1984 and 2008 using constructed time series of the different demographic parameters. The number of female offspring produced per female at age x (assuming a 1:1 male–female ratio at birth) was estimated as

$$m_x = 0.5 M_x F_x$$

with M_x representing the proportion of females that are mature at age x, and F_x being the potential fecundity of a female at age x.

The probability of surviving to age x (l_x) was calculated from the results of the SPA. Survival was divided into two categories: survival from birth to age 3 years (prerecruit age classes) and survival for age 3+. Survival from birth to age 3 years was calculated with the time series of the annual TEP and the abundance of cod of age 3. Survival over the first 3 years of life was estimated as

$$S_t = N_{3,t}/\mathrm{TEP}_{t-3}$$

with $N_{3,t}$ representing total abundance of age 3 fish in year t, and TEP_{t-3} the annual total egg production in year $t - 3$. Average annual total mortality (Z) in each of the 3 years was calculated as $-\ln S/3$. In the stock assessments of cod in both northern and southern Gulf of St. Lawrence, it was concluded that natural mortality in these stocks changed over time. Following examination of different model formulations for the SPA, the accepted model for both stocks included the estimation of M by the model (Swain and Chouinard 2008; Fréchet et al. 2009; Swain et al. 2009). Values of instantaneous rate of natural mortality ($M = 0.2$–0.4) consistent with the assessment were used to determine survival probability of age 3+ cod in the nGSL (Fréchet et al. 2009). Values of M of 3+ fish were then set at 0.2 prior to 1986, 0.4 from 1986 to 1996, 0.23 between 1997 and 2002, and 0.31 from 2003 to 2008. Diagnostic analysis of the SPA output indicated that the model formulation using variable M gave the best adjustment to the data with no retrospective patterns in both population numbers and fishing mortality. To determine the impact of fishing on population growth, instantaneous rate of population increase was also estimated using total mortality Z ($F + M$) obtained from the SPA. Age-specific survival for 3+ fish (l_x) using Z for each year was then used to re-estimate r denoted as r_Z.

Life table statistics were estimated for specific periods corresponding to the collapse of the stock (1986–1993), the period between the first and second moratorium (1994–2002), and the period following (2003–2008) the second moratorium. Mean reproductive rate, instantaneous rate of population increase, generation time, and doubling time of the population with the 95% confidence limits were calculated for each period using Monte Carlo analysis. Iterations (1000) using random values from a normal distribution for the mean age-specific survival and reproduction with their standard errors for each period were used for the calculations. Standard errors (SEs) for age-specific survival of 3+ fish were obtained from the estimates of SE for M in the SPA (Fréchet et al. 2009). SE for age-specific survival of 3+ fish based on Z was set to a value corresponding to the mean proportional estimates of SE for M (i.e., a similar coefficient of variation of 12.4%).

The sensitivity of the instantaneous rate of increase to survival probability and reproductive rate at age was determined by an elasticity analysis (Caswell 2001). The analysis evaluates the relative effect on r of proportional changes in single specific value of age-specific survival and reproduction, while all other values are held constant. The standard method for the calculation of elasticity values is found in Caswell (2001).

The recovery potential of the nGSL cod stock was examined using population projection matrix derived from life tables of age-specific survival and reproduction (Caswell 2001). A stochastic projection model using Monte Carlo simulation was used to predict changes in spawning stock numbers over time under different conditions of natural and fishing mortality. Spawning stock numbers were converted to spawning stock biomass (SSB) using mean mass-at-age of cod in the nGSL (Fréchet et al. 2009). Simulations were done using 1000 iterations of random values from a normal distribution for the mean age-specific survival and reproduction estimates. Mean values with SEs were calculated for the

2003–2008 period. Spawning stock numbers from the SPA and mass-at age in 2008 were used as starting values for the projections (Fréchet et al. 2009).

Life tables analysis and population projections were made using PopTools, an add-in tool for PC versions of Microsoft Excel (available for download from http://www.poptools.org).

Environmental conditions

Interannual variability of the cold intermediate layer (CIL) core temperature in the Gulf of St. Lawrence and mean yearly temperatures at specific depths of 150, 200, and 250 m were used as indices of environmental conditions. The CIL has been shown to be correlated with average winter air temperatures and associated with winter cold water volume and volume of Labrador Shelf water intrusion (Gilbert and Pettigrew 1997; Galbraith et al. 2008). Data were obtained from DFO, Atlantic Zone Monitoring Program (AZMP), and other DFO surveys (Galbraith et al. 2008).

Results

Condition factor

Marked changes in the condition factor of maturing cod were observed between 1984 and 2008 for both the early winter and prespawning period (Fig. 1). The condition factor of a standard 50 cm cod in January was high and relatively stable between 1984 and 1989. It declined afterwards to reach minimum values between 1992 and 1994. The condition of the fish improved at the end of the 1990s to levels similar to those observed at the beginning of the series.

The condition factor in January was significantly lower between 1991 and 1994 than in the preceding and following periods for each of the most abundant size classes (40, 50, and 60 cm size classes; Kruskal–Wallis tests, $p < 0.001$). In the month of May, the condition factor was lower in 1994 (Kruskal–Wallis tests, $p < 0.001$) than in all other years for all size classes.

The relationship between condition factor in the months of January and the following month of May (Fig. 2) was used to estimate the condition factor of reproductive cod in May for the period of 1984 to 1993 (Fig. 1). The relationship using mean condition factor in January and the following May for the different size classes representing the bulk of the spawning stock explained 74% of the variability in fish condition between the beginning of the overwintering and prespawning period (Fig. 2).

Interannual variation in the condition factor was significantly related to the temporal variations in the temperature conditions for the nGSL. Temperature anomaly for the CIL was positive between 1979 and 1985 (Fig. 3). Negative temperature anomalies were observed from 1986 to 1998, with lowest values in the period between 1992 and 1995. With the exception of 2003, temperature anomalies were positive after 1998. At depths of 150, 200, and 250 m, temperature anomalies were positive for most of the time before 1989. They were negative at each depth for most of the years between 1990 and 1998 and largely positive afterwards. Condition factor in January (year $t + 1$) was significantly related to temperature anomalies (year t) at depths of 150, 200, and 250 m, with coefficients of determination of 0.42, 0.50, and 0.54 ($p < 0.0001$), respectively. No autocorrelation was detected in any of the relationships (Durbin–Watson test; $p > 0.37$). No relation ($p > 0.079$) was observed between the condition factor and the temperature anomaly of the CIL, which represents the lowest temperature in the range of depths between approximately 30 and 120 m.

Fig. 1. Mean condition factor (K) of a 50 cm cod in January (●) and May (■) for the period between 1984 and 2008. For both series, mean K was calculated for maturing fish. Values of K in May for 1984 to 1993 (+) were obtained from the relationship between K in January and K in May estimated for years where data were available for both months between 1994 and 2007.

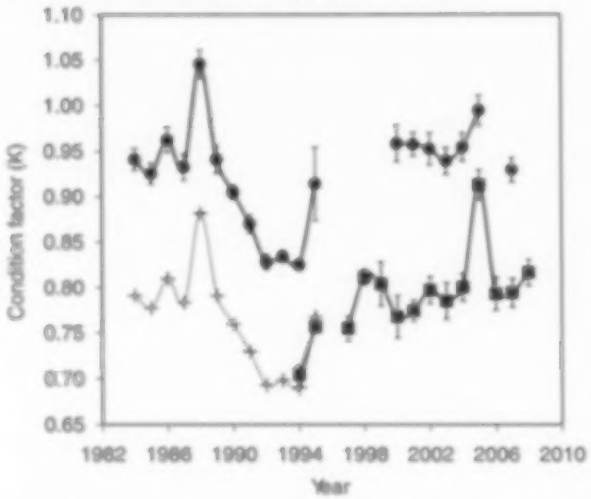
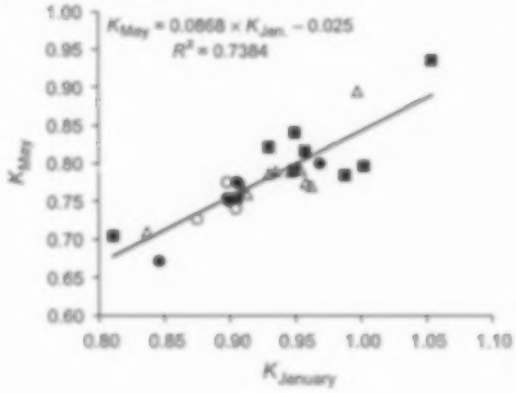


Fig. 2. Relationship between condition factor at the beginning of overwintering in January (K_{Jan}) and condition factor in the next spring during the prespawning period (K_{May}). The relationship was determined using the condition factors for the 40 (■), 50 (△), 60 (●), and 70 cm (○) size classes, these size classes representing the bulk of the reproductive fish.



Mean lengths-at-age

Lengths-at-age for cod of ages 5 to 8 varied among years, with lowest values observed in the year of 1988 and in the 1992–1994 period (Fig. 4). Clear significant decreasing trends were observed for each age between 1984 and 1994 (Kruskal–Wallis, $p < 0.001$). Since 1994, a significant posi-

Fig. 3. Time series of temperature anomalies at different depths and condition factor of a 50 cm cod in January in the northern Gulf of St. Lawrence between 1978 and 2007. Minimum temperature anomaly for the cold intermediate layer (CIL; ~30 to 120 m) and yearly average temperature anomalies at 150, 200, and 250 m are presented for each year along with condition factor observed in January of the following year ($K_{(y+1)}$). Temperature anomalies were calculated from mean temperatures measured during the 1971–2000 period. The solid horizontal line represents a zero deviation from the long-term mean. Temperature data were obtained from Galbraith et al. (2008).

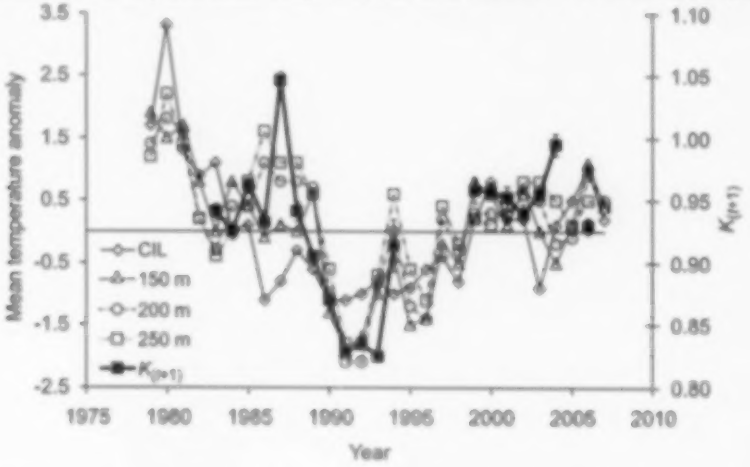
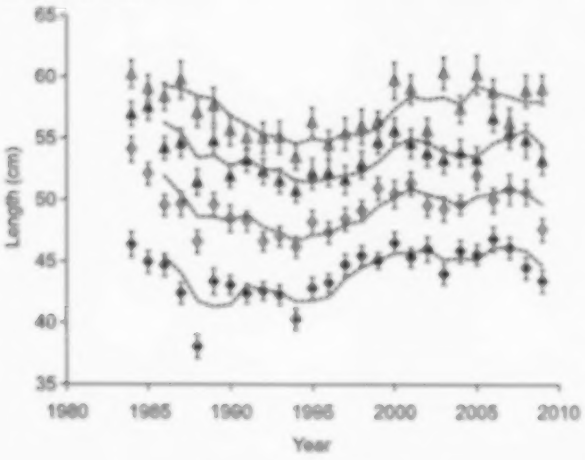


Fig. 4. Mean lengths (± standard error, SE) at ages 5 (◆), 6 (○), 7 (▲), and 8 (△) in the northern Gulf of St. Lawrence between 1984 and 2008. Observed lengths are presented for cod sampled in January and May, and corrected lengths (May equivalence) from July samples are presented for the years 1995 to 2001, 2003, and 2004. Mobile means with a 3-year path are used to show trends in length-at-age over time.



tive trend is observed for ages 5 and 6 cod. Multiple comparisons (Bonferroni correction) did not detect significant increases in length-at-age between 1994 and the period of 2005–2007 for cod of ages 7 and 8 except for the year 2005 where length-at-age of age 7 cod was significantly higher than in 1994. For all age classes, length-at-age in recent years (i.e., 2005–2007) is comparable ($p > 0.05$) to length-at-age observed at the beginning of the series (i.e., 1984–1986).

The statistical comparisons did not include corrected lengths-at-age obtained from data collected in July 1995 to 2001, 2003, and 2004. Mean relative growth rate for ages 4 to 11 was 1.63% (±1.2%) with no age effect on growth. This represents increases between 0.6 and 1.3 cm between May and July for younger (age 4) and older fish (age 11), respectively.

Maturity

The proportion of mature fish at size was significantly different between years ($\chi^2 = 1011$, df = 20, $p < 0.0001$). Mean length at 50% maturity (L_{50}) of female cod between 1984 and 1992 was in the range of 45.2–48.9 cm, after which it declined to minimum values of 36.9 and 37.2 cm in 1995 and 1997, respectively. Since 1998, L_{50} varied between 41.9 and 44.6 cm, with an increasing trend since 2004. However, L_{50} is still lower than in the 1980s. Corresponding ages at 50% maturity (A_{50}) varied between 4 and 6.3 years old (Fig. 5). A_{50} was relatively stable around 5.5 years between 1984 and 1993, decreased to a minimum of around 4 in 1995 and 1997, and increased to values between 4.6 to 5.1 during the 1998 to 2008 period. A_{50} in the 2000s is still 1 year younger than at the end of the 1980s and early 1990s.

Potential fecundity

Significant interannual variations in the potential fecundity of cod were observed between years (Table 2). No difference in the slopes of the relationships between potential fecundity and length (ln-transformed data) was observed between years ($F = 1.6$, df = 6, $p = 0.14$), while ANCOVA indicated significant year effect on the potential fecundity ($F = 17.92$, df = 6, $p < 0.0001$). Multiple comparison tests indicated that potential fecundity was lowest in 1995; intermediate in 2001, 2002, and 2004; and significantly higher in the years 1998, 2005, and 2006 ($p < 0.05$).

Predicted potential fecundities from the fecundity model using length and mean condition factor of the females for the years 2004 to 2006 were in close agreement with observed potential fecundities for these years. Differences be-

Table 2. Regression parameters of the relationships between potential fecundity and fork length (ln-transformed data) for cod sampled in the northern Gulf of St. Lawrence.

Year	Size range (cm)	n	b	a	r^2	p	50 cm	65 cm
1995	37–65	53	3.964	–2.744	0.70	<0.0001	349 150	987 835
1998	35–60	120	3.860	–1.891	0.72	<0.0001	545 473	1 501 740
2001	37–90	220	3.265	0.378	0.79	<0.0001	514 399	1 211 506
2002	36–65	72	3.527	–0.695	0.73	<0.0001	490 267	1 236 832
2004	43–103	120	3.754	–1.624	0.71	<0.0001	470 586	1 260 035
2005	37–87	100	3.675	–1.135	0.84	<0.0001	563 366	1 477 517
2006	36–90	125	3.600	–0.882	0.81	<0.0001	541 059	1 391 363

Note: Linear model: $\ln Y = a + b \ln X$. For each relationship, the year of sampling, size range of fish, the slope (b), the intercept (a), coefficient of determination (r^2), probability level of significance (p), number of fish (n), and the potential fecundity of a 50 and 65 cm cod are presented. Data for 1995 to 2002 were obtained from Lambert (2008).

Fig. 5. Age at 50% maturity of female cod in the northern Gulf of St. Lawrence between 1984 and 2008. Estimated length and age with 95% fiducial limits were obtained from logistic curves.

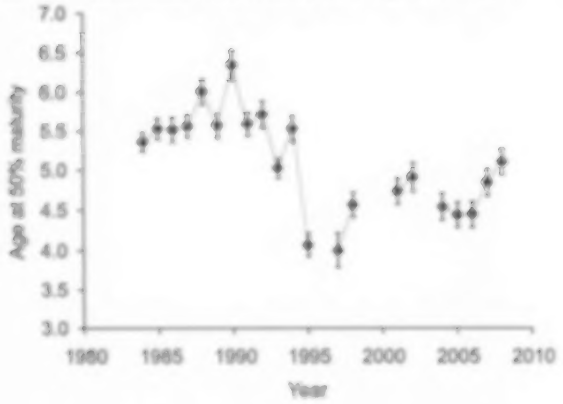
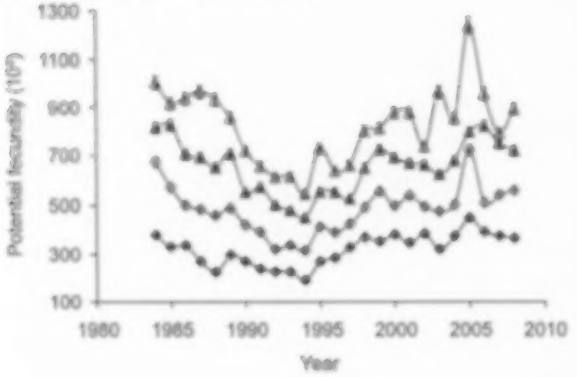


Fig. 6. Annual variation of the potential fecundity-at-age of female cod of ages 5 (◆), 6 (○), 7 (▲), and 8 (△) in the northern Gulf of St. Lawrence using the fecundity model with observed mean length and condition factor-at-age for each year.



tween estimated and observed values varied between 3% and 14% depending on length and year.

Time series of mean length-at-age and mean condition factor-at-age in the month of May were used as independent variables in the fecundity model to build the time series of potential fecundity-at-age (Fig. 6). While potential fecundity of a 50 cm cod decreased by 18% between the end of the 1980s and 1994, decreases in the order of 35% to 42% were observed in the potential fecundity-at-age for ages 5 to 8. Following 1994, a positive trend in the potential fecundity at length and age was observed. Potential fecundity in recent years has returned to values comparable to those observed at the beginning of the series (Fig. 6).

Annual total egg production (TEP)

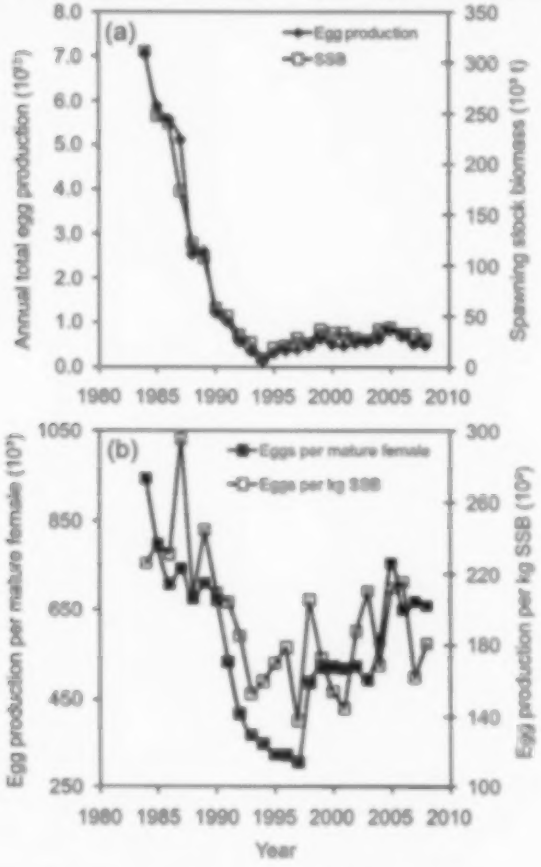
Annual TEP of cod in the northern Gulf of St. Lawrence followed the same declining trend as observed for the SSB between 1984 and 2008 (Fig. 7*a*). However, on a relative basis, marked changes in the reproductive potential were observed between the years (Fig. 7*b*). Mean egg production per mature female and mean number of eggs produced per kilogram of SSB decreased at the beginning of the 1990s to reach minimum values around the mid 1990s. An increase in these relative indices of egg production was observed in the 2000s, but the levels are still lower than those at the beginning of the series.

A positive relationship was observed between annual total egg production in year t and the number of recruits of age 3 in year $t + 3$ for the period between 1984 and 2008 (Fig. 8). For all years following 1989 when annual egg production was low, the number of recruits never exceeded 20×10^6 fish. However, differences in survival were observed during that period. Mean total mortality (Z) per year between birth and age 3 was equal to 4.55 (±0.106) between 1987 and 1995, while Z per year for the period between 1998 and 2008 was significantly (ANOVA, $F = 30.01$, df = 19, $p < 0.0001$) lower at a value of 4.32 (±0.08). Lowest Z per year in the series was observed in 1996 and 1997 with values of 4.03 and 3.89, respectively. Mean Z per year indicates that survival from birth to age 3 after 1998 was twice as high as that in the period from 1987 to 1995 (1.17×10^{-6} compared with 2.35×10^{-6}).

Intrinsic rate of population increase

Annual estimates of instantaneous rate of population increase (r) were highly variable between 1984 and 2008 (Fig. 9). Negative r values were observed for 10 consecutive years between 1986 and 1995, indicating that population numbers would have decreased even in the absence of fishing. Positive r was observed following the first moratorium (1994–1996), with values varying between 0.036 and 0.264. However, following the 1-year moratorium of 2003, lower

Fig. 7. Annual total egg production and spawning stock biomass (SSB) (*a*) and mean egg production per mature female and kilogram of SSB (*b*) of cod in the northern Gulf of St. Lawrence between 1984 and 2005. Mean egg production was estimated from annual total egg production of the stock and the number of mature females and SSB obtained from the sequential population analysis.



annual estimates of r were observed (0.036 to 0.083). Annual estimates of r_Z based on age-specific total mortality ($F + M$) of 3+ fish were negative for all years between 1984 and 1995. Following the 1994–1996 moratorium, r_Z varied between –0.092 and 0.193, with a negative trend since 2003. Fishing effort on the stock reduced the annual rate of increase from an estimated level of 5% in 2003 to –8.7% in 2008.

Mean reproductive rate, instantaneous rate of increase, and doubling time of population size differed markedly among the period of the collapse of the stock (1986–1993), the period between the first and the second moratorium (1994–2002), and the period from the beginning of the second moratorium (2003) and 2008 (Table 3). Mean reproductive rate during the decline of the stock indicates that expected numbers of female offspring produced by reproductive females during their lifetime were not enough to replace themselves (R_0 and $R_{0Z} < 1$). Instantaneous rate of increased (r_Z) was then negative, resulting in a mean decrease in population numbers per year of –30% (Table 3). The estimated rate of

Fig. 8. Stock–recruit relationship for northern Gulf of St. Lawrence cod between 1984 and 2008 estimated from annual total egg production in year $t - 3$ and recruits of age 3 in year t. A linear regression giving the best fit to the relationship ($R^2 = 0.94$) is represented by the dotted line.

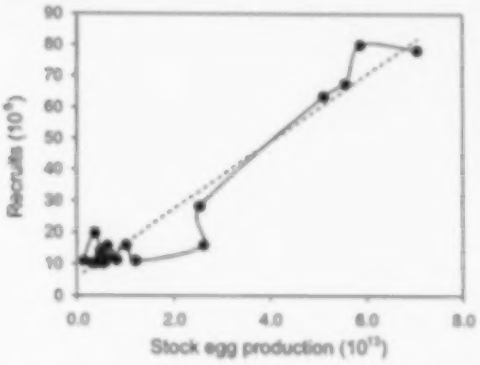


Fig. 9. Annual estimates of the instantaneous rate of population increase of cod in the northern Gulf of St. Lawrence for the period between 1984 and 2008 using yearly estimates of age-specific survival and reproduction. Age-specific survival was estimated for both natural mortality M (r) (●) and total mortality Z (r_Z) (○) at age. The dashed horizontal line indicates the level at which population numbers are stable.

decrease per year in the absence of fishing (r_{year}) indicates that 27% of the decrease in population numbers (r_{year}/r_{Zyear}) would not be associated with fishing mortality. Population numbers were estimated to decrease by half in 1.9 and 8.5 years in the presence and absence of fishing, respectively (DT_z and DT). In the 1994–2002 period, the absence of fishing for a period of 3 years (1994–1996) and the improvement in life history characteristics resulted in higher reproductive rate (R_0 and $R_{0Z} > 1$) and positive instantaneous rate of increase. Despite a 1-year moratorium in the 2003–2008 period, mean reproductive rate and instantaneous rate of increase, although positive, were similar or slightly lower than in the preceding period. Mean R_{0Z}, r_Z, and doubling time of population numbers indicate that population numbers were essentially stable (Table 3). The absence of fishing might have resulted in a rate of increase in population num-

Table 3. Life table statistics of cod in the northern Gulf of St. Lawrence for the time period when the stock collapsed (1986–1993), between the first and second moratorium (1994–2002), and from the second moratorium onward (2003–2008).

	1986–1993	1994–2002	2003–2008
Age-specific *M*			
R_0	0.424 (0.300; 0.575)	2.657 (1.535; 4.371)	1.988 (1.32; 2.515)
r	–0.086 (–0.117; –0.055)	0.100 (0.044; 0.163)	0.070 (0.044; 0.097)
r_{year}	–8.2 (–11.1; –5.3)	10.6 (4.5; 17.7)	7.3 (4.5; 10.1)
G	10.7 (10.1; 11.2)	8.8 (8.0; 9.6)	9.2 (8.8; 9.7)
DT	–8.5 (–12.7; –5.9)	8.5 (4.2; 15.9)	10.5 (7.2; 15.9)
Age-specific *Z*			
R_{0Z}	0.085 (0.055; 0.120)	1.32 (0.744; 2.145)	1.029 (0.782; 1.312)
r_Z	–0.361 (–0.417; –0.308)	0.033 (–0.038; 0.105)	0.002 (–0.032; 0.035)
r_{Zyear}	–30.3 (–34.1; –26.5)	3.4 (–3.8; 11.1)	0.2 (–3.1; 3.5)
G_Z	7.3 (7.0; 7.7)	7.3 (6.8; 7.8)	7.8 (7.5; 8.2)
DT_Z	–1.9 (–2.2; –1.7)	–35.8 (–71.9; 100.0)	–14.0 (–244.0; 275.7)

Note: Reproductive rate (R_0 and R_{0Z}), instantaneous rate of increase (r and r_Z), increase in population numbers (percentage per year; r_{year} and r_{Zyear}), generation time (G and G_Z), and doubling time in population numbers (DT and DT_Z) are calculated for age-specific natural mortality (M) and age-specific total mortality Z ($M + F$). Mean values with 95% confidence limits in parenthesis are presented.

bers of 7% per year with a doubling time of 10.5 years. Finally, generation time based on age-specific natural mortality indicated that the mean age of reproductive females produced by the offspring of a cohort was between 8.8 and 10.7 years compared with 7.3 to 7.8 years when G was estimated with age-specific total mortality.

The elasticity analysis indicated that age-specific survival had a proportionally larger influence on r and r_Z than age-specific reproduction (Fig. 10). The elasticity of r and r_Z to survival declined with age, while elasticity of r and r_Z to reproduction increased to a maximum at ages 6 to 8 and then declined. The analysis is only presented for the data of the 2003–2008 period, as almost identical results were obtained for the other periods.

Population projections using Leslie matrix indicate a slow recovery of the SSB of cod in the nGSL in the absence of fishing and a complete absence of rebuilding of the stock if the fishing mortality levels of 2007–2008 (catches of ~6200 t) were to be maintained (Fig. 11). Stochastic projection of population growth using mean age-specific natural mortality and reproduction (maturity and fecundity) for the 2003–2008 period (Table 4) indicates that the SSB would increase from the estimated level of 29 650 t in 2008 to an SSB of 63 520 t (95% confidence interval, CI: 58 987 to 67 977 t) after 10 years and to 121 641 t (95% CI: 109 229 to 135 153 t) after 20 years. This represents a mean rate of increase in population size of 7.2% per year, with a doubling time of 9.9 years. Stochastic projection of population growth using age-specific total mortality (Z; Table 4) indicates that age-specific fishing mortality resulting in a mean F for ages 7 to 11 of 0.40 in 2007–2008 does not allow any rebuilding of the stock. Maintaining the same level of fishing mortality would result in a decrease in population size of –0.3% per year.

Discussion

Changes in life history traits affecting reproductive potential will have strong repercussions for population dynamics and sustainable harvesting. In the nGSL, condition factor, lengths-at-age (i.e., growth), potential fecundity, and age–length at maturity that are important in determining the reproductive potential of cod all reached minimum values in the early 1990s. These low values coincided with a period when temperature conditions in the Gulf of St. Lawrence where below normal. These conditions combined with a high fishing intensity resulted in a rapid collapse of the stock. From 1983 to 1994, the total biomass (3+ fish) decreased from 602 000 to 22 000 t (DFO 2009), representing an instantaneous rate of change in population numbers of –0.27 per year (slope of regression of $\log_e$ abundance in numbers versus time in years). The close relationships between temperature and life history traits determining reproductive potential support the hypothesis that poor environmental conditions significantly contributed to the collapse of the cod stock in the nGSL.

Condition factor has been shown to be a very reliable estimate of the energy content for cod (Lambert and Dutil 1997*a*, 1997*b*), and numerous studies showed that it influences growth (Dutil et al. 1999), fecundity (Lambert and Dutil 2000), reproductive potential (Scott et al. 2006; Lambert 2008), swimming performance (Lapointe et al. 2006), susceptibility to diseases (Dutil et al. 2006), and survival (Dutil and Lambert 2000; Scott et al. 2006). The relationships between condition factor and temperature anomalies demonstrate the impact of the cooling of the water masses in the nGSL on the productivity of the stock. The exact mechanism linking condition factor to temperature is hard to determine. Lower condition may result from decreased metabolic rate of the fish at lower temperature, lower food intake due to lower productivity of the entire ecosystem, modifications in the distribution and abundance of prey, changes in the migration patterns of cod affecting prey availability, or more probably a combination of all these causes (Lambert and Dutil 1997*b*; Castonguay et al. 1999; Rothschild 2007). Nevertheless, as a result, lower condition was associated with lower size-at-age, fecundity, and egg production. Estimates of total mortality from catch curves during the 1994–1996 moratorium on nGSL cod were also higher than 0.5, suggesting an increase

Fig. 10. Elasticity of the instantaneous rate of increase for the 2003–2008 period to age-specific survival (squares) and reproduction (diamonds). Elasticity values are presented for instantaneous rate of increase estimated from natural mortality (closed symbols) and total mortality (open symbols).

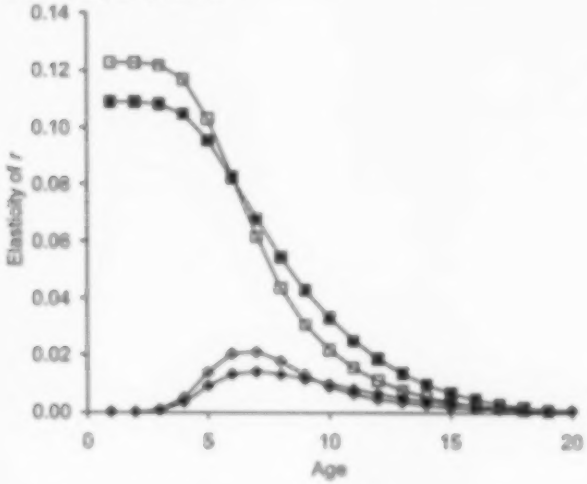
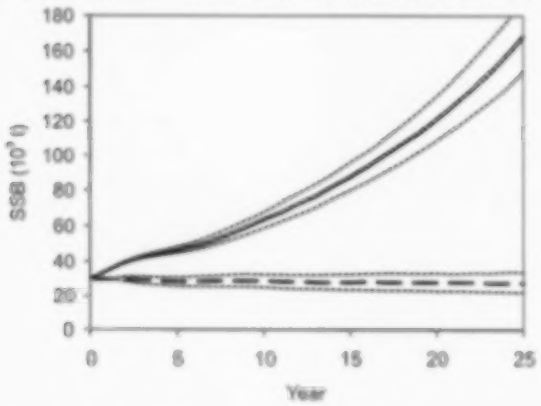


Fig. 11. Expected change in spawning stock biomass (SSB) over time in the absence of fishing (solid line) and with a mean fishing mortality (ages 7 to 11) of 0.4 (dashed line). SSB is estimated from Leslie matrix projection of age-specific survival and reproduction using mortality and mean reproductive parameters for the 2003–2008 period. A stochastic projection using Monte Carlo simulation was used to determine mean SSB with 95% confidence intervals.



in natural mortality (Benoît and Chouinard 2004; Grégoire and Fréchet 2005; Shelton et al. 2006). Given the very low total catches (148–367 t) during that period, the increase in natural mortality to a value of 0.4 during the collapse of the stock is sound.

Instantaneous rates of population growth (r) indicate that the stock biomass would have decreased even in the absence of fishing during the late 1980s and early 1990s. The negative annual estimates of r observed for 10 consecutive years clearly demonstrate that the productivity of the stock was lower during the period when the stock collapsed. Comparison of mean r and r_Z suggests an important negative environmental impact on the stock productivity during that period. Mean rate of decrease per year (–8.2%) associated with natural mortality (r) represents 27% of the mean rate of decrease per year (–30.3%) associated with total mortality (r_Z) for that period. Negative r could also be observed in the presence of strong density-dependent effects when carrying capacity is reached. However, the very low abundance levels observed for the stock do not support this possibility.

Table 4. Mean age-specific mortality and reproduction with standard errors for cod in the northern Gulf of St. Lawrence.

Age	M	Z	m_a
0	4.36±0.077	4.36±0.077	0
1	4.36±0.077	4.36±0.077	0
2	4.36±0.077	4.36±0.077	0
3	0.31±0.028	0.31±0.038	3 435±1 474
4	0.31±0.028	0.32±0.040	27 690±11 031
5	0.31±0.028	0.35±0.044	107 010±31 515
6	0.31±0.028	0.44±0.054	225 594±39 846
7	0.31±0.028	0.51±0.063	351 268±43 752
8	0.31±0.028	0.65±0.081	481 861±51 819
9	0.31±0.028	0.89±0.110	617 865±66 247
10	0.31±0.028	0.77±0.095	763 087±89 701
11	0.31±0.028	0.73±0.090	915 537±124 043
12	0.31±0.028	0.51±0.063	1 073 600±169 958
13	0.31±0.028	0.51±0.063	1 235 567±227 471
14	0.31±0.028	0.51±0.063	1 399 834±296 294
15	0.31±0.028	0.51±0.063	1 564 983±375 968
16	0.31±0.028	0.51±0.063	1 727 798±465 907
17	0.31±0.028	0.51±0.063	1 893 258±565 426
18	0.31±0.028	0.51±0.063	2 054 528±637 765
19	0.31±0.028	0.51±0.063	2 212 932±790 110
20	0.31±0.028	0.51±0.063	2 367 935±913 613

Note: Age-specific natural mortality (M) and reproduction (m_a) were estimated for the period between 2003 and 2008, and age-specific total mortality (Z) was estimated using age-specific fishing mortality observed for the years 2007 and 2008.

As demonstrated by the elasticity analysis, estimates of population growth in the absence of fishing (r) are more sensitive to changes in age-specific natural mortality (M) than to changes in age-specific reproduction. However, elasticity analysis does not take into account that the variability in the different parameters may not be proportional and that these parameters may covary (Caswell 2001). Although not supported by the different studies conducted on cod populations in the Gulf of St. Lawrence (Grégoire and Fréchet 2005; Swain and Chouinard 2008; Fréchet et al. 2009), the use of a constant M of 0.2 for adult fish (i.e., 3+) to estimate r annually would nevertheless indicate that r was 58% to 64% lower during the period when the nGSL cod stock collapsed. Each variation in M of a value of ±0.1 keeping all other parameters constant would result in a change in r corresponding to a variability in population growth of approximately ±7% per year. Given this relative importance of M in determining r, further studies on interannual variation in M, on age-specific variability in M, and on the relationships among growth, reproduction, and mortality should be encouraged.

These results based on the analysis of the life history characteristics of the stock corroborate the conclusion based on changes in biomass, surplus, and net production hypothesiz-

ing that the environment played a major role in the collapse of cod stocks in the northwest Atlantic. Estimates of surplus and net production per capita indicated that the productivity of nGSL cod in the second half of the 1980s and in the early 1990s was nil or even negative (Dutil et al. 1999). From the examination of the net productivity of several Atlantic cod populations, it was also concluded that for five stocks located in the Gulf of St. Lawrence and around the Grand Banks and Labrador, the stock biomasses in the late 1980s and early 1990s would not have increased in the absence of fishing (Hilborn and Litzinger 2009).

While environmental conditions substantially contributed to the collapse of the stock, fishing mortality appears to be the major limiting factor for the rebuilding of nGSL cod stock and the only one that can be managed. Following 1998, the higher temperatures were associated with increases in the condition factor, sizes- and fecundity-at-age, and survival probability, with lower Z from birth to age 3 and lower M (0.20 to 0.28) for age 3+ fish. These changes resulted in an increased reproductive potential and positive annual estimates of r, indicating that in the absence of fishing, the population size would have potentially increased at a mean rate between 7% and 11% per year. However, a decreasing trend in annual estimates of r is observed since 1998. Considering the fishing effort on the stock, annual estimates of instantaneous rate of population growth (r_2) varied between –0.09 and 0.09 with a declining trend since 2003, representing decreases in numbers from 5% to –8.7% per year. Comparison of r and r_2 indicates that fishing mortality is largely contributing to the absence of rebuilding of the stock since the reopening of the fishery in 1997. However, there are indications that the productivity of the stock (i.e., r), although higher than in the 1990s, might not have returned to levels observed before the collapse. Lengths-at-age and age and length at 50% maturity for nGSL cod were greater in the 1970s, while natural mortality was estimated to be lower (0.15 to 0.2) in the same period (Minet 1978; Dutil et al. 1999). Assuming some trade-off between growth and reproduction, the lower age and length at maturity of cod in the nGSL for the recent period would be consistent with a growth deficit (i.e., cost) increasing with age as demonstrated by the steeper decreasing trend in length-at-age for older fish in the 1974–1994 period (Dutil et al. 1999). The intrinsic rate of natural increase, r, derived from the spawner–recruit relationship of cod in the nGSL for the 1970–1990 period, which was estimated to be equal to 0.20 (Myers et al. 1997), also supports this conclusion.

Changes in length-at-age (i.e., growth) and age–length at maturity may represent phenotypic and (or) genetic response to the environment and fishing pressure (Law 2000; Ernande et al. 2004; Dieckmann and Heino 2007). However, disentangling evolutionary changes from phenotypic plasticity is a major difficulty. It is predicted that increased fishing pressure favors maturation at younger age and smaller size, since fishing may generally result in the selective removal of fast-growing individuals (Law 2000; Heino and Dieckmann 2008). The earlier age and smaller size at maturity of Atlantic cod off Labrador and Newfoundland were explained by a hypothesis of a genetic response to fishing-induced selection against late-maturing and large-maturing genotypes (Hutchings 1999; Olsen et al. 2005). The continued small size-at-age of the collapsed cod stock in the southern Gulf of St. Lawrence (sGSL) despite little fishing was also seen as a result supporting the hypothesis of a genetic change in response to size-selective fishing (Swain et al. 2007). However, laboratory experiments with cod of the same stock origin demonstrated that the maximum growth capacity of sGSL cod was comparable to other stocks in the Atlantic, including some not considered to have been overexploited (Dutil et al. 2008). It was concluded that these results were not consistent with the hypothesis that intense size-selective fishing resulted in a loss of the innate growth capacity. In the nGSL, there is no evidence from the analysis of cumulative mortality of cohorts, selectivity of the different fishing gears, and changes in the relative importance of fishing gears over time that the fishery was selectively removing fast-growing individuals (Dutil et al. 1999). In a review of size-selectivity patterns in major commercial fisheries, it was found that the intensity of selection and the size selectivity were both considerably less than those used in laboratory experiments to demonstrate evolutionary changes (Hilborn and Minte-Vera 2008). The lack of any relationship between exploitation rate and change in mass suggested that the observed changes in mass (i.e., growth) were more probably due to ecological than evolutionary factors.

The higher total mortality per year (Z) between birth and age 3 during the period when nGSL cod collapsed could potentially indicate a size-selective pressure on immature and slow-growing cod in the mid-1980s and early-1990s. Total mortality between birth and age 3 includes mortality at the egg and larval stages and seal predation on juvenile cod. Harp seal population in the northwest Atlantic increased from less than 2 million individuals in the 1970s to almost 6 million individuals in 2005, with 25%–33% of the population migrating in the nGSL (Hammill and Stenson 2005). It was estimated that 95% of cod found in harp seal stomachs were less than 38 cm, with ages 1 and 2 fish representing 75% of total cod consumed (Chassot et al. 2009). Cod biomass removed by seal predation was estimated to vary between 10 000 and 30 000 t for the period of 1985 to 2000.

Finally, the close relationship between lengths-at-age and temperature and the rapid increase in lengths-at-age and age–length at maturity following the moratorium observed in the present study would best be explained by phenotypic plasticity allowing cod to respond quickly to changes in fishing pressure and environmental conditions (Trippel 1995; Law 2000; Ernande et al. 2004). However, long-term trends in lengths-at-age and age–length at maturity (i.e., since the 1970s) might indicate that some evolutionary changes are also acting.

The relative importance of the environment and fishing effort on the collapse and absence of recovery of cod in the nGSL could reflect the situation of many of the northwest Atlantic cod stocks. All these stocks collapsed at about the same time in the mid-1990s (Shelton et al. 2006). Concomitant with the rapid decline in stock sizes associated with high fishing mortality, higher natural mortality, slower growth, and earlier age–size at maturity were observed in many of these stocks (Shelton et al. 2006). Important negative temperature anomalies were also reported on a large scale in the northwest Atlantic from the mid-1980s to the mid-1990s (Colbourne 2004; Drinkwater and Gilbert 2004). This coherence

between cod stock dynamics and temperature conditions was interpreted as an evidence suggesting that the environment had a stronger role in explaining the 1985–1992 declines in cod abundances than previously thought (Rothschild 2007).

The use of demographic analysis represents a useful and alternative tool to measure stock productivity and disentangle environmental and fishing effects on population abundance. For example, the combined effects of increased natural mortality, decreased body growth, earlier age and size at maturity, and reduced recruitment rates that are put forward to explain the lower productivity of the cod stocks in the northwest Atlantic (Sinclair 2001; Chouinard et al. 2005; Shelton et al. 2006) can be estimated with a single measure: the instantaneous rate of increase r. Moreover, the use of time series to obtain annual estimates of r is incorporating interdependence between these life history traits. For example, based on life history theory, one could expect that with a decrease in age–size at maturity, adult growth and future fecundity should decrease while mortality should increase (Stearns 1992). Empirical estimates of r will include these interrelations.

Population projection using mean age-specific survival and reproduction for the recent period (2003–2008) also provides a measure of the rebuilding potential of the stock. Under the current set of life history characteristics and in the absence of fishing, the mean instantaneous rate of population growth was estimated at 0.07 with a doubling time of 10 years, while achieved rate of increase maintaining the actual age-specific fishing mortality (i.e., mean F for ages 7 to 11 of 0.40) is nil. Since the end of the 1994–1996 moratorium, each time total catches exceeded ~5000 t for consecutive years, a decline in the SSB was observed (DFO 2009). Based on abundance estimates, a 5000 t catch represents an F value of ~0.27. Thus, a significant reduction in fishing effort would have a positive effect on the rebuilding of the stock. However, given the low abundance level of the stock and the low instantaneous rate of increase, approximately 22 years without fishing would be necessary to reach the 140 000 t limit reference level of SSB (DFO 2009) that has been calculated for this stock.

Although density-dependent effects can be incorporated into demographic models (Caswell 2001), the present study was based on a classic demographic analysis (i.e., density independence), as no evidence of density effects and large deviation from stable age distribution were detected for the period of time under study. It can be safely argued that the nGSL cod stock is well below the carrying capacity of the environment, as the biomass of the stock (3+ fish) since 1994 only represents 3.5% to 11% of the observed biomass in the 1980s (Fréchet et al. 2009). The relationship between stock egg production and recruits (present study) and the different models of stock–recruit relationships indicating that changes in the relationships only occurred above a reference level of SSB of 200 000 t (Duplisea and Fréchet 2010) do not provide evidence of density-dependent effects on the stock–recruit relationship for the period covered in the present study. Variations in lengths-at-age (i.e., growth), fecundity, and natural mortality for the time series examined (1984–2008) are not consistent with density effects where reduced survival, growth, and fertility are expected at higher fish density. Moreover, no relation was observed between cod growth and stock abundance in the Gulf of St. Lawrence for the period between 1978 and 1995 (Dutil et al. 1999; Swain et al. 2003). Without negating possible density dependence, it can nevertheless be concluded that possible deviations from the assumptions underlying the use of the present demographic model are not important enough to invalidate its use in the present study.

Demographic models using empirical estimates of life history characteristics could well be used to define rebuilding strategies for depleted stocks. Instantaneous rate of increase resulting from an observed set of life history characteristics and initial indices of population size could be used to set a growth trajectory necessary to reach a determined population level in a specific time period taking into account the health of the stock as well as social and economic pressures. During the recovery period, a regular monitoring of r and abundance indices could be used to adjust fishing effort to maintain the planned population growth trajectory.

Population response to variations in stock reproductive potential in different environmental conditions and under different fishing pressure can be evaluated using matrix population models given that some knowledge of density-dependent effects are known. Models linking the influence of the environment to survival, growth, age–size at maturity, and fecundity could provide estimates of the rate of increase and resilience of populations to harvesting for specific combination of life history traits and environmental conditions.

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A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (*Pagrus auratus*)

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Abstract: Intraspecific variation in movement patterns are well established for many species, but poorly appreciated in fisheries management. In this study we dart-tagged snapper (*Pagrus auratus*), an important fishery species, across different areas and habitats in the Hauraki Gulf, New Zealand. Tag returns were used to quantify movement behaviour and extraction rates using a maximum likelihood model that corrected for spatial variability in population size and fishing effort. Residency was high (~90%) in two strata and lower (75%) in the remaining stratum. The stratum with the highest residency also appeared to experience the highest extraction rate (likely due to a lower population size). These results confirm the existence of differences in movement behaviour within the snapper population, suggesting that localized areas may become depleted regardless of the status of the overall stock. This has consequences for the scale of fisheries management and the size of marine reserves implemented in different regions. Understanding why variation in movement behaviour exists (i.e., genetic vs. environmental) is the next step in addressing the influence of animal behaviour on fisheries management.

Résumé : Les variations intraspécifiques dans les patrons de déplacement sont bien connues chez plusieurs espèces, mais mal comprises dans la gestion des pêches. Dans notre étude, nous avons marqué avec des étiquettes à dard des pagres (*Pagrus auratus*), une espèce importante pour la pêche commerciale, dans des sites et habitats différents dans le golfe de Hauraki, Nouvelle-Zélande. Les retours d'étiquettes ont servi à déterminer le comportement de déplacement et à calculer les taux d'extraction à l'aide d'un modèle de vraisemblance maximale qui tient compte de la variabilité spatiale de la taille de la population et de l'effort de pêche. Le taux de résidence est élevé (~90 %) dans deux des strates et plus faible (75 %) dans la troisième. La strate avec le taux de résidence le plus élevé semble aussi connaître le taux d'extraction le plus fort (vraisemblablement à cause d'une population plus petite). Ces résultats confirment l'existence de différence de comportements de déplacement dans la population de pagres, ce qui laisse croire que des sites particuliers peuvent devenir dépeuplés, quel que soit le statut du stock dans son ensemble. Cela a des conséquences sur l'échelle de la gestion de la pêche et sur la taille des réserves marines établies dans les différentes régions. La prochaine étape consiste à comprendre pourquoi il existe une variation dans le comportement de déplacement (c'est-à-dire le rôle relatif des causes génétiques par rapport aux causes environnementales) pour évaluer l'influence du comportement animal sur la gestion des pêches.

[Traduit par la Rédaction]

Introduction

Intraspecific variation in movement behaviour or partial migration (the existence of both resident and migratory movement patterns within a single species) is well documented (e.g., insects: *Schistocerca gregaria* (Rainey 1976, 1978); birds: *Accipiter gentilis* (Newton 1979), *Fringilla coelebs* (Newton 1979), *Somateria mollissima* (Milne and Robertson 1965); reptiles: *Geochelone gigantea* (Swingland and Lessells 1979); fish: *Gasterosteus aculeatus* (Bell 1976); and mammals: *Connochaetes taurinus* (Talbot and Talbot 1963)). One of the best examples of intraspecific variation comes from the salmon family. Most species of Pacific salmon express some variability in movement behaviour, but none as much as the sockeye salmon (*Oncorhynchus nerka*). Sockeye have forms that are resident in fresh water (kokanee) or anadromous, and different populations of sockeye spend varying lengths of time in fresh water before conducting spawning migrations to the sea (Behnke 2002).

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While intraspecific differences in movement patterns appear common, with underlying mechanisms having been investigated over a period of greater than 20 years (e.g., Gaines and McClenaghan 1980; Swingland 1983), appreciation of within species variability in movement is less prevalent in some areas of research than others. While there are a growing number of examples of marine fish with varied movement behaviours (e.g., galjoen, *Dichistius capensis* (Attwood and Bennett 1994); many South African sparids (Griffiths and Wilke 2002); Atlantic cod, *Gadus morhua* (Robichaud and Rose 2004); some Jamaican reef fish (Munro 2000: in sensu Gell and Roberts 2003); and snapper, *Pagrus auratus* from western Australia (Moran et al. 2003) and New Zealand (Parsons et al. 2003; Egli and Babcock 2004)), it is still standard practise for fisheries assessments to ignore movement variability (see Hilborn and Walters (1992) for examples of factors commonly incorporated into fisheries assessments). By not accounting for movement variability, there is a risk that detrimental consequences, such as localized depletion of highly residential animals (Parsons et al. 2009), may occur. In addition, maintaining resident and migrant contingents within a population may be important for mediating population stability (Kerr et al. 2009). Incorporating variation in movement behaviour into the design of marine reserves may also ensure all movement contingents are afforded protection within those reserves (Kramer and Chapman 1999; Parsons et al. 2010). Finally, fisheries-induced selection, which has been shown to act on life history characteristics such as size (Hilborn and Walters 1992) and growth rates (Conover and Munch 2002), may also differentially select behaviour types, reducing behavioural biodiversity with the potential for cascading effects throughout the ecosystem.

The New Zealand snapper (*P. auratus*: Sparidae) is an exploited marine fish species, and both circumstantial evidence and tagging studies suggest that intraspecific variation in movement behaviour exists. Fishermen categorize snapper as either "school" fish, which are thought to follow seasonal migrations, or resident, so-called "kelpy" snapper, which are thought to remain year round in areas of rocky reef. Previous tagging studies have provided evidence for both behaviour types, but these studies were conducted separately and used different methodologies. Large-scale mark–recapture programs have observed movements of up to 418 km (Paul 1967), provided evidence supporting seasonal onshore–offshore movements (Crossland 1982), and suggested that most tagged snapper were recaptured within 10–20 km of the release location (Gilbert and McKenzie 1999). Alternatively, acoustic tagging of snapper in rocky reef habitat has shown that snapper can be resident to areas with dimensions of only a few hundred metres (Parsons et al. 2003; Egli and Babcock 2004). While variation in movement behaviour within the snapper population seems apparent, previous investigations have not been designed or analysed to assess whether the variation in movements could be associated with particular areas or habitats. For example, previous mark–recapture studies have largely avoided tagging snapper in areas of rocky reef (Gilbert and McKenzie 1999), whereas the acoustic tagging studies were largely focused within one rocky reef system inside a single marine reserve. Therefore, it was the aim of this study to make direct comparisons of the movements of snapper from different areas and habitat types where we expected differences in movement behaviour to exist. This would also allow us to compare extraction rates among areas, which may provide an indication of how differences in movement behaviour influence vulnerability to exploitation.

Materials and methods

Tag release and recovery

Between October 2006 and March 2007, we tagged 5983 snapper throughout the Hauraki Gulf, New Zealand, using external dart tags. We used yellow Hallprint (South Australia) plastic tipped dart tags with a 9 cm streamer. Each tag had a unique four digit tag number printed on either end of the tag and the phrase "NIWA Prize Draw Ph 09 3752050". Snapper were caught for tagging by chartering commercial longliners. Each longliner would set ~2500 baited hooks each morning (between 0300 and 0700) and then immediately begin retrieving the hooks (which would usually be completed before 1400). Longlining was selected as the preferred method of capturing snapper for tagging because longline-caught snapper usually incur little injury and have a high survival probability after release (Davies et al. 1999). As snapper were brought aboard, they were carefully handled using rubber gloves and placed in a flow-through seawater tank. Snapper were then retrieved from the tank, measured, and vented with a hypodermic needle if the swim bladder appeared to be distended. Using a tag applicator, each fish received a dart tag in the dorsal musculature, with the dart locking between the pterigiophores, before the fish was released over the side. A global positioning system (GPS) location was recorded for every 20th fish that was tagged.

Snapper were tagged in three strata within the Hauraki Gulf: Inner Gulf, Mid Gulf, and Reef (Fig. 1). The Reef stratum was constrained to areas close to the shoreline (<1 km from land) that were dominated by structurally complex rocky reef habitat. Alternatively, the Inner Gulf and Mid Gulf strata were dominated by soft sediment (although some structural components such as sponges, horse mussels (*Atrina zelandica*), and cobbles are present), and we actively avoided setting lines over hard bottom where it was present. The Inner and Mid Gulf strata were separated from each other largely on the basis of depth (the strata boundary mostly followed the 20 m depth contour).

Fishermen (both recreational and commercial) who captured tagged snapper would contact the phone number on the tag with the incentive of winning the prize draw of fishing tackle that we gave away each month. We advertised the tagging program through interviews on multiple radio programs and television fishing shows, articles in news papers and fishing-oriented magazines, advertisements in popular fishing tackle shops, and by handing out thousands of flyers at boat ramps throughout the Hauraki Gulf. For the purposes of the current study, only tags recaptured during the period November 2006 to October 2008 have been included in analyses. When fishers contacted us about tagged snapper, we asked them for the tag number, the location and date of capture, as well as some other pertinent questions. This information was then mailed to the fisher for verification. In addition, we included a map for each fisher to place a mark

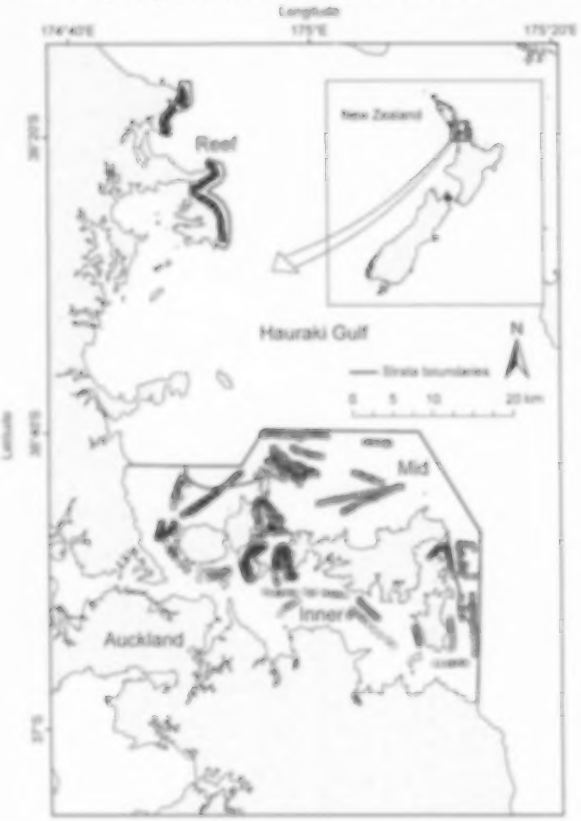


Fig. 1. Location map showing New Zealand (inset), the Hauraki Gulf, the three tag release strata, and the locations of all tag releases (Inner: open circles; Mid: grey, filled squares; and Reef: filled triangles). Tags were released over multiple tagging voyages spanning the following dates: 6 November 2006; 4 December 2006 – 7 December 2006; 12 February 2007 – 16 February 2007; 22 February 2007 – 23 February 2007; 19 March 2007 – 22 March 2007.

of where the tagged snapper had been caught, as well as a postage-paid, self-addressed envelope, in which all of the above information and the tag itself was placed and mailed back to us. At this stage, the fisher was put into the prize draw and sent a thank you letter.

Once we had obtained all the recapture information, it was associated with the release information for the same tag, and the positions of release and recapture were plotted in a geographic information system (GIS). As we only recorded the release locations for every 20th snapper (generally separated by <250 m), we estimated the release locations of the other tagged snapper by assuming that all the tagged snapper between the two recorded positions had been released with even spacing and in a linear fashion. For the location of recapture, we utilized the positions obtained from the fishers maps and entered those coordinates into our GIS.

Standardization of tag returns

Tag recovery data is not only dependent on where tagged fish move to, but also on the probability that a tagged fish will be recaptured, which can vary spatially. There are two main factors that can alter this recovery probability: the population density of other snapper and the amount of fishery extraction. Therefore, to accurately compare the dispersal probability of snapper populations within each of the release strata at the time of tagging, we needed to correct for the influence that population density and fishery extraction would have on tag recoveries throughout the area that tagged snapper moved through. As a result, we developed a method, described below, that not only accounted for population density and fishery extraction at the locations of recapture, but also took their values into account throughout the entire fishery.

To estimate the fishery extraction of snapper within our tag recovery area (the fishery area between North Cape and East Cape on the North Island of New Zealand, otherwise known as SNA1), we obtained the location and mass (kg) of snapper caught by commercial fishing operations for the period October 2007 to September 2008. Approximately 80% of the commercial fishing effort targeting snapper is reported with exact coordinates of fishing locations. We assumed the distribution of these known fishing locations was representative of all commercial fishing effort for snapper and adjusted the catches at the known locations to represent the entire commercial catch mass. For recreational fishers, we conducted boat ramp surveys throughout and aerial flights over the Inner and Mid Gulf areas over the 2007–2008 fishing year (October 2007 through September 2008 inclusive) following the methods of (Hartill et al. 2007). Estimates of recreational fishing effort and catch for the entire northeast coast of the North Island were obtained during the 2004–2005 fishing year using the same methodology. We compared the estimated tonnage of snapper landed within the Inner and Mid Gulf areas over the 2007–2008 fishing year against the 2004–2005 fishing year estimates for the same area. This ratio was then used to create an estimate of the tonnage of snapper landed by recreational fishers for the entire northeast coast of the North Island in 2007–2008. This tonnage was then prorated by effort across the locations where recreational fishing vessels had been recorded in the 2004–2005 survey. While it was not ideal to combine estimates from surveys conducted in different years, the spatial distribution of recreational fishing effort is not expected to vary greatly from year to year, as it is largely determined by proximity to urban areas (B.W. Hartill, personal observation). Therefore in the absence of complete spatial coverage in one survey, the most prudent approach was to prorate the level of catch observed during the tag recovery period over the spatial distribution of effort experienced in a previous survey. Overall, our estimates suggested that in northeast New Zealand between October 2007 and September 2008, commercial and recreational fishers caught 4474 and 3443 t of snapper, respectively. The recreational and commercial snapper extraction layers were then combined to provide a complete estimate of snapper extractions throughout the tag recovery area.

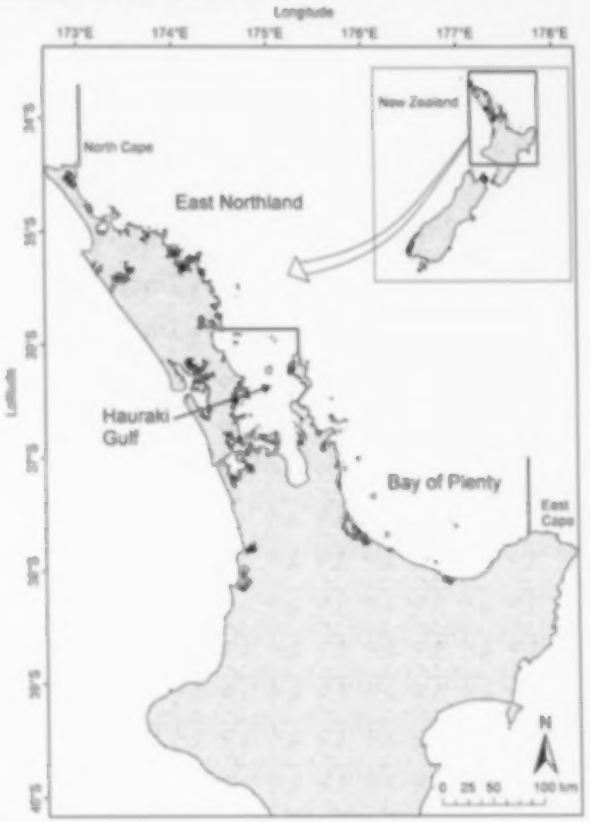
To estimate the spatial distribution of snapper population density, we assumed that commercial bottom longlining catch per unit effort (CPUE) would estimate the abundance of snapper at the locations where those longlines were set. We therefore compiled observations of CPUE (kilograms of snapper per number of hooks) from all commercial longlining during the 2007–2008 period and also from the longlining activities conducted as part of the tag release phase. As

we did not weigh snapper from the longline sets we conducted as part of the tagging phase, we converted the lengths of all the snapper caught to masses using the regression equation described by Paul (1976). All of these CPUE observations were associated with the latitude and longitude of the start position for each longline set. For each of the CPUE and catch data sets, we created a raster layer with 10 km grid cells that encompassed the snapper fishery between North Cape and East Cape (otherwise known as the SNA1 fishery). Along the edges of tag release strata, raster grid cells that overlapped more than one stratum were split along the boundaries of that stratum, and the area calculations for those specific cells adjusted accordingly where required. For CPUE, the value of each raster cell was determined by the average of all the CPUE estimates that fell in that cell, while for catch, the cell value was determined by the sum of all snapper catch that fell within that cell. On average, snapper catch was ~20 t per 10 km grid cell, while the average grid cell value of CPUE was ~0.15 kg snapper per hook. Fish abundance and fishery extraction are likely to vary seasonally, therefore having an inconsistent effect through time on the probability that a tagged fish will be recaptured. Ideally, we would have assessed the influence of season on movement, but this was prevented by incomplete coverage of longline CPUE data when divided seasonally. It is also possible that longline efficiency may vary spatially or among different habitat types. Commercial longliners operate throughout the SNA1 area, however, and good catches and high gear efficiency are possible in all habitat types (D.M. Parsons, personal observation)

Movement estimation

Movement estimates were derived for each of the three tagging strata (Reef, Inner, Mid; Fig. 1), which were treated independently (i.e., reciprocal movements were not explicitly estimated). For each of these release strata, tagged snapper were able to move to four possible recovery areas defined as follows: the original release stratum (did not move), Hauraki Gulf (the other two release strata plus the remainder of the Hauraki Gulf), east Northland, and Bay of Plenty (see Figs. 1 and 2 for representation of tagging strata and recovery area boundaries). Movement was derived as the proportion of the population resident within the release stratum at the time of tagging that could be found within the recovery area of interest (including the original release stratum) at any one instant during the recovery period. By definition, all movement proportions had to sum to one (including the proportion of the population that did not move). These estimates of fish movement will likely vary during such a long recovery period (2 years), as (*i*) fish movement among recovery areas may well be seasonal, and (*ii*) fish movement between distant strata does not happen instantaneously. Considering the latter of these points, it is likely that the time required for fish movements (including long distance movements) to reach equilibrium is small relative to the overall recovery period. Seasonal movements, however, are likely to exist within our tagging results (Crossland 1982). We did not have the resolution to investigate seasonality in movements because there were too few tag returns to divide seasonally. The movement results we present are therefore a cumulative movement probability over the entire 2-year recovery period and likely encompass two seasonal movement cycles.

Fig. 2. Map of New Zealand (inset) focusing on northeastern New Zealand (SNA1) and the boundaries of the three recovery areas (in addition to the release strata).



Stratum proportional movements were estimated using a negative binomial, negative log-likelihood function with the following parameterisation: M_j is the total number of tagged fish released in stratum j; P_{jk} is the probability a fish tagged in stratum j would move to recovery area k; C_{ik} is the snapper catch in recovery area k, raster-grid cell i; X_{ik} is the catch rate (commercial longline CPUE) in the ith raster-grid cell in recovery area k; r_{jik} is the actual number of fish tagged in stratum j recaptured in the ith raster-grid cell in recovery area k; a_{ik} is the area (km^2) of the ith raster-grid cell in recovery area k; q is longline catchability (an unknown parameter for which it is assumed that the average population size (kg) in the ith raster-grid cell in recovery area k during the recovery period is $qX_{ik}a_{ik}$); c is a factor allowing for tag loss, tagging and natural mortality, and under-reporting; q' is a nuisance parameter, defined as

$$(1) \qquad q' = c/q$$

that is, a combination of both unknown parameters; s is the shape parameter for the negative binomial; W_k is a factor, defined as

$$(2)\qquad W_k = \frac{\sum_i C_{ik}}{\sum_i X_{ik} a_{ik}}$$

which determines the relative likelihood that a fish will be caught, given that it is in recovery area k (also referred to as relative fishing effort); U_j is the recovery period extraction rate for fish that were in stratum j at the time of tagging (i.e., the proportion of these fish that were caught during the recovery period); and U_{ik} is the recovery period extraction rate for fish in the ith raster-grid cell in recovery area k, assumed to be given by

$$(3)\qquad U_{ik} = \frac{C_{ik}}{qX_{ik}a_{ik}}$$

The expected number of fish tagged in stratum j that moved to recovery area k ($E(M_{jk})$) is given by ($M_j P_{jk}$). This assumed that fish tagged in stratum j were distributed over recovery area k in proportion to abundance, where the expected number of fish tagged in stratum j that were in the ith raster-grid cell in recovery area k (e_{jik}) during the recovery period (ignoring tag loss and tagging and natural mortality) is given by

$$(4)\qquad e_{jik} = \frac{(M_j P_{jk}) X_{ik} a_{ik}}{\sum_i X_{ik} a_{ik}}, \text{ where } \sum_{ik} e_{jik} = M_j$$

Furthermore, the expected number of fish tagged in tagging stratum j that were reported as caught in the ith raster-grid cell in recovery area k ($\hat{r}_{jik}$) is given by

$$(5)\qquad \hat{r}_{jik} = \frac{c e_{jik} C_{ik}}{q X_{ik} a_{ik}} = \frac{q' e_{jik} C_{ik}}{X_{ik} a_{ik}}$$

while the negative log-likelihood (λ_j) for r_{jik} is given by the negative binomial distribution (F) specified as follows:

$$(6)\qquad \lambda_j = -\sum_{k,i} \log\left[F(r_{jik}, \hat{r}_{jik}, s)\right]$$

where

$$(7)\qquad F(r, \hat{r}, s) = \frac{\Gamma(r+s)}{\Gamma(s)\Gamma(r+1)} \frac{s^s \hat{r}^r}{(s+\hat{r})^{s+r}}$$

Therefore,

$$(8)\qquad \hat{r}_{jik} = \frac{q' M_j P_{jk} C_{ik}}{\sum_{i,k} X_{ik} a_{ik}}$$

and the expected number of fish tagged in tagging stratum j that were reported as recaptured in recovery area k ($\hat{r}_{jk}$) is given by

$$(9)\qquad \hat{r}_{jk} = q' M_j P_{jk} W_k$$

where

$$(10)\qquad \hat{r}_{jk} = \sum_i \hat{r}_{jik}$$

Estimatable parameters were P_{jk} (vector of proportional movements) and the constants q' and s ($k + 2$ parameters). A likelihood penalty term was added to constrain the sum of all proportional movements from j to equal one. This model assumes the proportional movement vector estimates for each stratum are independent. This is because the q' and s constants are shared across all j release strata; therefore, it was convenient to estimate all movement vectors using one overall combined likelihood (θ) given by

$$(11)\qquad \theta = \sum_j \lambda_j + 1000\left[\left(\sum_k P_{jk}\right) - 1\right]^2$$

In addition to estimating movement probabilities, we also estimated the exploitation rate of tagged fish for each release stratum. This exploitation rate represents the probability that a fish from stratum j is captured during the recovery period (about 2 years), regardless of location. We calculated this exploitation rate using the ratio of tagged fish that had been captured compared with the number originally released in each stratum as given by

$$(12)\qquad \mu_j = \frac{r_j}{M_j}$$

Final estimates of the exploitation rate of tagged fish also incorporated adjustments for tagging-related mortality, tag loss, and tag under-reporting. Specifically, the total number of snapper tagged in a stratum (M_j) was adjusted for tagging-related mortality on the basis of survival estimates specific to the depth each tagged fish was captured from. These estimates were based on a holding experiment conducted by Davies et al. (1999) and range from 1.4% to 11.6% mortality. The number of recaptured snapper (r_j) was also adjusted to compensate for tag loss (12%) and tag under-reporting (15%), as suggested by Davies et al. (1999).

An alternative analysis approach would have been to estimate movement and exploitation simultaneously in an integrated analysis (e.g., Maunder 2001). One of the main advantages of such an approach is that it incorporates uncertainty around observational data (e.g., catch and CPUE) and produces a more holistic understanding of the uncertainty around the parameters of interest that the model generates. Such an approach, however, was beyond the scope of the current study. An integrated analysis, however, has been previously conducted for the SNA1 fishery (Bentley et al. 2004), but did not provide a great level of detail on snapper movements. Despite these alternative approaches, the analysis method presented here represents a novel way of adjusting for factors that have the potential to be highly influential on raw tag return information.

The movement model was constructed using ADModel Builder software (Otter Research Ltd., Sidney, British Columbia). Maximum likelihood estimates (MLE) were derived using autodifferentiation minimization. Estimates of variation around movement probabilities and exploitation rates were derived from Markov chain Monte Carlo (MCMC) resampling of the model parameter space (10 000 draws from 1 000 000 MCMC likelihood samples). We tested the goodness of fit of the model by calculating the expected number of cells in which 0, 1, 2, 3, etc. tagged fish were recaptured and compared this with the observed distribution of tag recaptures for each release stratum (Fig. 3). Expected and observed distributions showed a close match, suggesting the model was performing well. An assumption of this movement model is that longline catchability (q) and the factor allowing for tag loss, tagging and natural mortality, and under-reporting (c) are constant spatially and temporally.

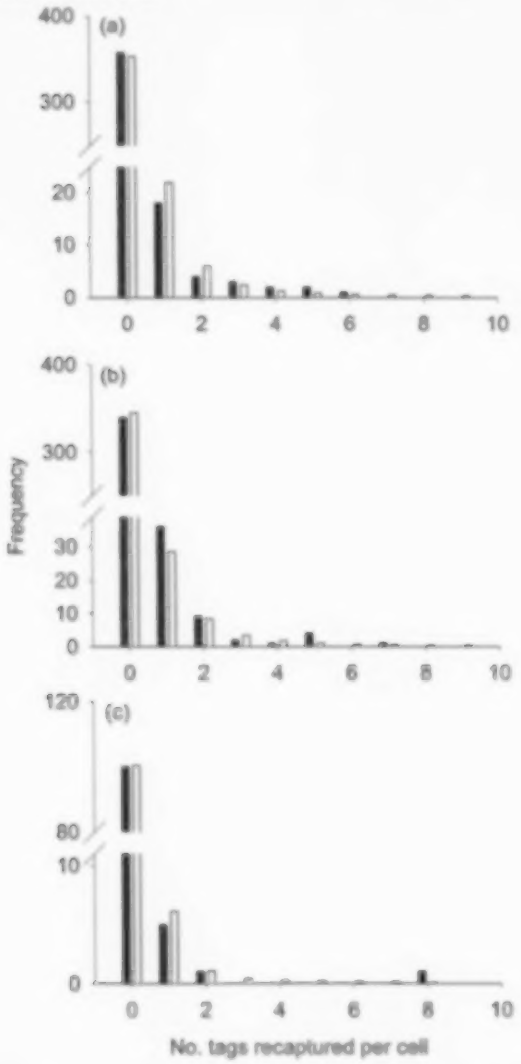


Fig. 3. Goodness of fit comparison for the observed number of tags returned from each cell (filled bars) compared with the number predicted by the model (open bars) for the (*a*) Inner, (*b*) Mid, and (*c*) Reef release strata.

We also assessed the effect of fish size and time at liberty on the distance between release and recapture. This was conducted using simple linear regressions comparing the fork length (FL, cm) of the fish tagged and the time at liberty (days) with the distance moved (km) between release and recapture for each release stratum.

To test for significant differences in movement probabilities, MCMC estimates of the proportion of the population within their original release stratum (i.e., an indication of residency) were compared with the same estimate for all other release strata. Specifically, this was done by ordering MCMC estimates from lowest to highest and establishing the value of the lower and upper 95th percentile. These percentiles were then compared between release strata, and if no overlap occurred, we attributed this as a significant difference in movement between the two release strata concerned. Our hypothesis for this test was that snapper from structurally complex reef areas would be resident, while snapper from soft sediment areas would be more mobile, potentially following seasonal migrations. No such significance test was possible for the comparison of exploitation rates for tagged fish, as we used raw data in its calculation (i.e., there was no estimate of variation). In terms of exploitation rate, we anticipated higher exploitation in reef areas where fish were resident and therefore exposed to fishing effort in that location year round.

Results

Of the 5983 snapper tagged, 373 were recovered by recreational and commercial fishermen between November 2006 and October 2008 (Table 1). The distance moved between tagging and recapture ranged from zero movement to 410 km. There appeared to be a pattern in the location of recaptures dependent on which stratum tagged fish were originally released in (Fig. 4). For example, snapper tagged within the Reef stratum were most often recaptured within their stratum of release (median distance moved = 0.7 km, 25th percentile = 0.4 km, 75th percentile = 1.6 km; Fig. 4*a*), whereas snapper tagged in the Mid stratum were often recaptured within the Hauraki Gulf and to a lesser extent in the Bay of Plenty and East Northland (median distance moved = 18.9 km, 25th percentile = 5.9 km, 75th percentile = 80.7 km; Fig. 4*b*). Snapper tagged within the Inner stratum exhibited a level of mobility in-between the other two strata and were also most often recaptured within their stratum of release, while some fish were recaptured within the Hauraki Gulf and Bay of Plenty (median distance moved = 3.6 km, 25th percentile = 1.2 km, 75th percentile 7.0 km; Fig. 4).

When this raw movement information (based on the number of snapper released and recaptured from each release stratum and recovery area) was compared with the model's prediction of movement (P_{ij}), there were some large differences (up to −186%) (Table 1). These differences largely occurred because the model predicted that a larger proportion of the original population within each release stratum would remain there compared with the raw tag return information. The results of the movement model, however, confirmed that the proportion of the population from each stratum that could be found within their release stratum was dependent on which stratum they were originally released in (Table 2, Fig. 5). For example, snapper released in the Reef stratum were more likely to be found within their release stratum than snapper released in the Inner stratum (Table 2). Variance in the proportion of the population from each stratum that could be found within their release stratum also differed among each release stratum. For example, snapper tagged in the Reef stratum showed high residency with low variance, while snapper tagged in the Mid stratum showed lower residency but more variance in terms of the likelihood of being found in other recovery areas (Fig. 5).

The exploitation rate of tagged fish (after adjusting for initial mortality, tag loss, and under-reporting) from each of the release strata over the 2-year recovery period varied from 6.8% for snapper populations from the Mid stratum to 10.1%

Table 1. The number of snapper tagged and recaptured by release stratum and respective recovery areas, with other pertinent response variables and model output.

	Recapture area			
		Hauraki Gulf	East Northland	Bay of Plenty
Inner release stratum	**Inner**			
No. of tags released	3444			
No. of tags recovered	184	34	1	8
Exploitation rate of tagged fish	8.6314			
Raw movement ratio	0.8106	0.1498	0.0044	0.0352
Predicted movement probability (P_{jk})	0.9191	0.0469	0.0038	0.0275
% Difference (raw – predicted)	–13.3851	68.6916	13.6364	21.8750
Relative fishing effort (W_k)	6.9359	2.4262	1.1122	0.9241
Mid release stratum	**Mid**			
No. of tags released	1820			
No. of tags recovered	24	49	1	17
Exploitation rate of tagged fish	6.7836			
Raw movement ratio	0.2637	0.5385	0.0110	0.1868
Predicted movement probability (P_{jk})	0.7539	0.1125	0.0071	0.1212
% Difference (raw – predicted)	–185.8930	79.1086	35.4545	35.1177
Relative fishing effort (W_k)	5.5558	2.5537	1.1122	0.9241
Reef release stratum	**Reef**			
No. of tags released	719			
No. of tags recovered	48	7		
Exploitation rate of tagged fish	10.0719			
Raw movement ratio	0.8727	0.1273		
Predicted movement probability (P_{jk})	0.9566	0.0434		
% Difference (raw – predicted)	–9.6138	65.9073		
Relative fishing effort (W_k)	5.0763	2.6454		

Note: The exploitation rate of tagged fish over the 2-year recovery period was calculated from the ratio of observed tag returns but adjusted for initial mortality, under-reporting, and tag loss. Raw movement ratio was calculated as number of tags from an area/total number released. Predicted movement probability (P_{jk}) was that generated by the movement model. The percent difference in movement probability was calculated as the percentage of the raw movement probability that the difference between the raw and predicted probabilities formed. Relative fishing effort (W_k) is the ratio of catch to relative abundance (standardized by area) for each release stratum.

for snapper populations from the Reef stratum (Table 1). We were not able to test whether these differences in the exploitation rate of tagged fish were significantly different, as the raw calculation of exploitation rates from tag return data did not provide any estimate of variance.

We also assessed the influence of fish size and time at liberty on the distance between release and recapture. In no instance did linear regression produce an r^2 value greater than 0.08.

Discussion

This study has demonstrated that the movement behaviour and exploitation rate of a commercially important fish species can be variable. Specifically, while snapper from certain areas restricted their movements to a scale of hundreds of metres (Reef stratum median distance moved = 0.7 km), snapper from an adjacent, but spatially separate, location moved over a scale of tens of kilometres (Mid stratum median distance moved = 18.9 km). Previous evidence suggesting differential movement patterns within the snapper population was accumulated over multiple studies (Crossland 1982; Gilbert and McKenzie 1999; Parsons et al. 2003). The current study, however, demonstrated intraspecific variation in movement behaviour, or partial migration, by concurrently tagging snapper in different areas with the same tagging methodology and while accounting for potentially influential factors (i.e., population size and catch). A major contribution of the current study was the tagging data analysis method that we utilized. Its importance was most clearly illustrated by the difference in movement estimates compared with when population size and catch were not accounted for. Specifically, interpretation of raw tag returns consistently underestimated the proportion of a stratum's population that remained within the stratum of release compared with model results (suggesting release strata had lower catch than the other recovery areas). We therefore recommend, where the data allow, that tagging studies aimed at estimating movement probabilities incorporate population size and catch.

Before tagging of snapper took place, we hypothesized that snapper tagged in areas of structurally complex rocky reef would be highly residential compared with snapper tagged in soft sediment areas. This made sense because (*i*) it agreed with the anecdotes of fishermen and previous studies of snapper movement (Crossland 1982; Gilbert and McKenzie 1999; Parsons et al. 2003), (*ii*) structurally complex habitats often have higher associated invertebrate and fish biomass (Stoner and Lewis 1985; Dean and Connell 1987; Friedlander and Parrish 1998), potentially providing more resources in a smaller area (or home range), and finally,

Fig. 4. Location of tag recaptures for (*a*) the portion of the Hauraki Gulf near the release strata and (*b*) the rest of SNA1, including East Northland and the Bay of Plenty. Strata boundaries are denoted by solid line, and strata of release are denoted as follows: Inner (open circles), Mid (grey filled squares), and Reef (filled triangles).

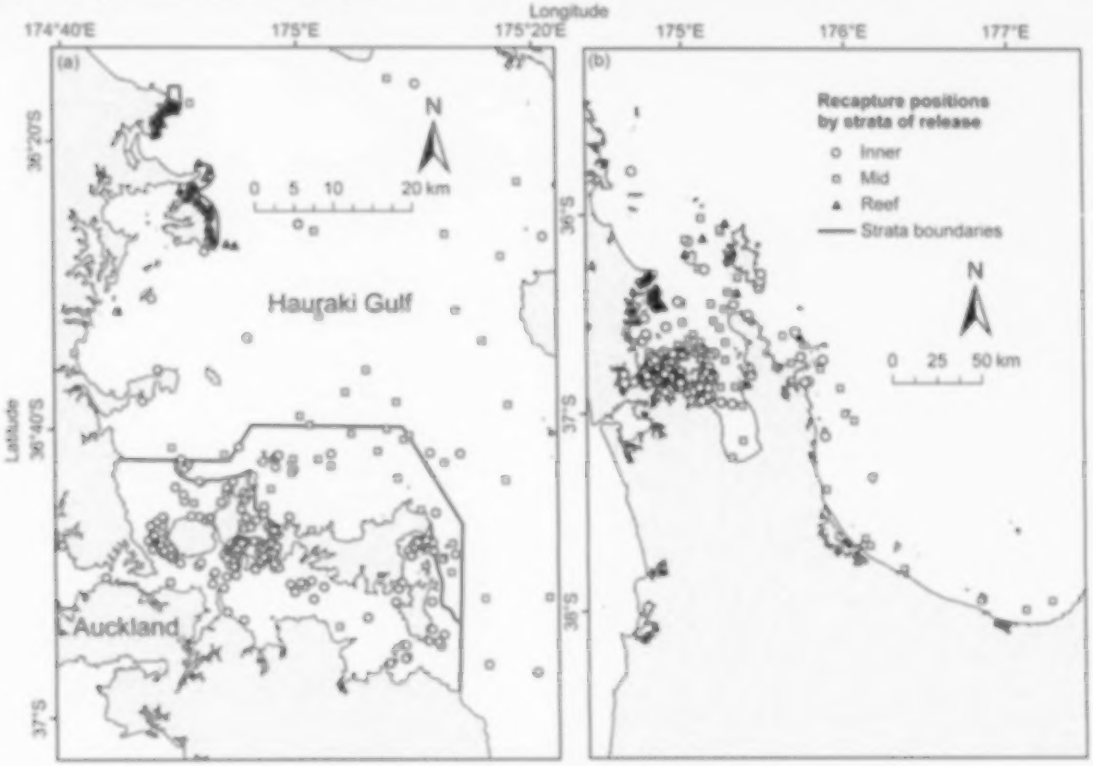


Table 2. Pairwise comparison of the proportion of the population from each stratum that could be found within their stratum of release.

	Inner	Mid	Reef
Inner	0.8575 to 0.9550	NS	NS
Mid	—	0.5876 to 0.8612	S
Reef	—	—	0.9044 to 0.9823

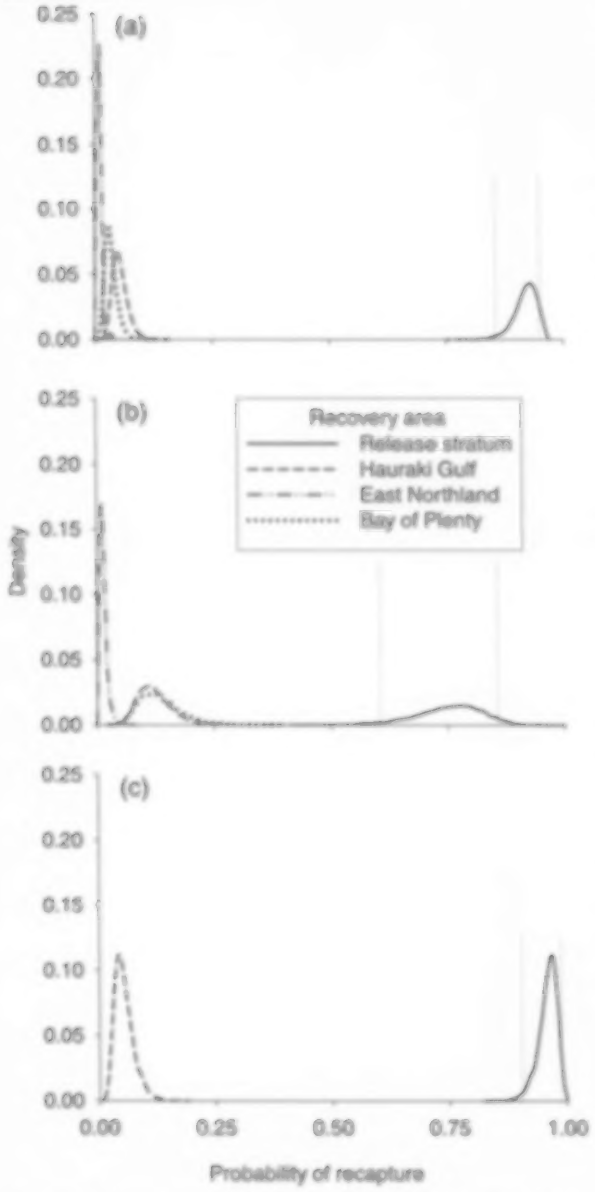
Note: Values illustrated along diagonal contain 95% of all Markov chain Monte Carlo (MCMC) replicates. S, significant difference between release areas at the 0.05 level of confidence; NS, no significant difference.

(*iii*) if structurally complex rocky reef habitats do contain more resources, they are likely to be high quality habitat patches and encourage site attachment (Rodenhouse et al. 1997). Our results agree with our initial hypothesis in that nearly all snapper from rocky reef areas were highly residential. Snapper from the Mid stratum were more mobile. Given that this stratum is dominated by soft sediments, habitat type may indeed be an important determinant of snapper movement behaviour.

Snapper from the Mid stratum were the most mobile. It is likely that many of these snapper were tagged during the inshore phase of an annual migration. There are multiple lines of evidence indicating that migratory behaviour is present within the snapper population (recreational fisher catch rates (Millar et al. 1997); baited video estimates of snapper abundance (Willis et al. 2003); previous tagging studies (Crossland 1982)). If snapper tagged in the Mid stratum were migratory, we would have expected few snapper to be present there during winter. This is supported by the poor catch rates experienced by research longlining conducted in the Mid stratum during winter 2007 (2.85 snapper per 100 hooks; D. Parsons, unpublished data).

Variation in movement behaviour, as demonstrated in the current study, begs the question "why do differences in movement exist within the same population?" Disentangling the likely contributions of genetic and environmental influences is not possible given our current understanding. At one extreme, genetics may be the dominant influence, with some individuals programmed to be mobile and others not. Such a genetic polymorphism could be maintained within the population through frequency-dependent selection (Wilson et al. 1994). Alternatively, environmental control may be more important. For example, if high-quality habitats become overcrowded, new arrivals may fare better in less crowded

Fig. 5. Density distributions of the average proportion of the population from each release stratum ((*a*) Inner, (*b*) Mid, or (*c*) Reef) that could be found within each recovery area (defined as P_{jk} in the Methods section). Density distributions for each recovery area were generated from 10 000 Markov chain Monte Carlo (MCMC) replicates of P_{jk} (with a bin size of 0.01). Vertical dotted lines represent the 95th percentiles of the estimates for the release stratum of concern. Note that each release area was also a possible recovery area (but see Figs. 1 and 2 for the spatial definition of the possible recovery areas).



locations (Fretwell and Lucas 1970). This interaction of habitat quality and population density may lead to exploration or dispersal, with residency adopted when suitable high-quality habitat with lower population density is located (Swingland 1983). An alternative explanation is that movement behaviour changes ontogenetically. This is unlikely, however, as we observed no correlation between fish size and distance moved (for the subadult and adult snapper we tagged).

Regardless of whether a genetic component contributed to the observed behavioural variation, fisheries-induced selection (not evolution) may still be able to alter the behavioural diversity within the snapper population in a temporary fashion. Fisheries-induced selection has been documented for other characteristics of exploited fish populations (Heino and Godø 2002) and has potentially detrimental consequences for fisheries (Hutchings 2005). If selection is acting on a nongenetic characteristic, this may lead to short-term consequences for the environment and stakeholders (i.e., before population replenishment occurs).

For fishery-induced selection to occur, different components of the snapper population must be exposed to different fishery exploitation rates. We originally hypothesized that the most resident fish would be exposed to the highest levels of exploitation. While we were not able to test for significant differences in exploitation rate, the high level of exploitation documented for the Reef stratum was concerning, considering the low overall fishing effort that occurred in that stratum (B.W. Hartill, unpublished data; also, compare values of W_k in Table 1). It is possible that catchability varied among strata, driving the high exploitation rate of tagged fish relative to fishing effort. A more parsimonious explanation, however, is that the population size of snapper in the Reef stratum was much smaller relative to the other strata, resulting in a higher mark rate, which in turn led to a higher exploitation rate. The influence of population size on the exploitation rate of tagged fish is likely to be further exacerbated in areas such as the Reef stratum, where restricted movements reduce the overall population that tagged fish mix amongst. Furthermore, if areas with low population density are generally composed of individuals with reduced movement capacity, this may suggest that these small resident populations are more vulnerable to localized depletion (i.e., a small amount of fishing effort is still capable of removing a large proportion of a small population).

The exploitation rate of snapper has been previously estimated, using a different method, for one of the areas where snapper were tagged in the current study. Willis and Millar (2005) calculated that 86% of snapper (within an area that encompassed the Reef strata) were removed by fishing activity over the summer period each year. Comparatively, the current study directly observed a much lower exploitation rate (10% exploitation over a 2-year period). We suggest these differences may be due to different behavioural responses to the camera system used by Willis and Millar (2005) (inside vs. outside of reserves, but see Peterson and Black (1994) for a detailed explanation of interactions between treatment levels and experimental artefacts). Variability in the approachability or "boldness" of adult snapper has been documented within a marine reserve (Cole 1994) and likely exists between reserve and nonreserve locations (D.M. Parsons, personal observation). As a result, Willis and Millar (2005) may have underestimated the nonreserve snapper population, leading to the exploitation rate being overestimated. This highlights the importance of understanding behavioural variation to fisheries management.

Given the results of the current study, it is possible that reasonably discrete and small populations of resident snapper may experience overexploitation while removals from the entire stock remain sustainable. The relative vulnerability of these resident populations will likely be strongly influenced by their proximity to urban centres, with areas close to cities experiencing higher fishing effort. Beyond these direct extraction effects, there may also be detrimental consequences for the maintenance of ecosystems at a localized scale. For example, it is likely that only resident snapper help to maintain algal productivity in rocky reef habitats in northeastern New Zealand (Shears and Babcock 2002). From a social perspective, localized depletion of fisheries resources will likely impact some stakeholders more than others. This is due to recreational and customary fishers concentrating the majority of their fishing effort at inshore locations (B.W. Hartill, unpublished data), where residential snapper are more likely to occur. As a result, it is likely that the stakeholder groups that fish in inshore areas make a major contribution to any overexploitation that occurs in those areas. Replenishment of snapper populations in areas that have been overexploited may occur relatively quickly in some locations, however. At the Poor Knights Islands Marine reserve, snapper populations increased by 450% within a year (Denny et al. 2004). This may suggest that mobile snapper are able to change behaviour type and take up residency. If "plastic" shifts in behaviour (Scheiner 1993) are supplementing inshore populations of resident snapper, then this may alleviate the ecological and social ramifications of localized depletion.

Fisheries managers may wish to address the potential for localized depletion and the environmental and social consequences that it may cause. To do so, more information on the dynamics of partial migration in exploited fish stocks will be required. Specifically, a better understanding of behavioural shifts and their contribution to replenishing resident populations and the influence of fishery selectivity on the prevalence of different movement contingents may be required. Monitoring programs may also need to be established to quantify the level of extraction that certain areas can sustain before overexploitation occurs. Such a research program may lead to finer scale spatial zoning with the intention of avoiding problems occurring on a localized scale. One part of this strategy may be to prioritize some areas near urban centres for only recreational and customary fishing, but with much lower daily catch limits. Marine reserves may also be an option to ensure that localized depletion does not occur, at least within the bounds of the protected areas. Failure to incorporate movement behaviour in reserve design, however, could lead to incorrectly scaled reserves (reserves of the size that currently exist in northeastern New Zealand (~5 km length) would afford little protection to mobile snapper from soft sediment areas). Therefore, the implementation of reserves will also require an adequate appreciation of movement behaviour and how this varies with habitat type. Whatever action is taken, decisions will ultimately come down to a balance of values. This study has demonstrated that certain environmental and stakeholder values can be threatened even when total extraction from a fishery is sustainable. The challenge will be whether these other values are worth consideration.

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Environmental and maternal effects on embryonic and larval developmental time until dispersal of lake sturgeon (*Acipenser fulvescens*)

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Abstract: For migratory fish like lake sturgeon (*Acipenser fulvescens*), the period from egg deposition through embryonic and larval development until dispersal (ELDTUD) contributes substantially to variation in survival at the individual level and to population levels of recruitment. Using genetically determined parentage, we examined the relative importance of environmental variables in a stream environment (e.g., temperature and discharge) and maternal effects (including individual female body size, spawning time, and location) to ELDTUD on an individual basis. Adult lake sturgeon (n = 208) spawning in the Upper Black River (Michigan, USA), and larvae (n = 1444) dispersing downstream were captured during the 2007 spawning season. We used generalized mixed models and multimodel inference based on Kullback–Leibler information-theoretic criteria to demonstrate that environmental variables and the maternal effects of individual female and spawning time were both important predictors of ELDTUD. Decreasing ELDTUD during the season resulted from linearly increasing temperature and nonlinearly decreasing river discharge. Spawning time and individual female explained a large proportion of variation in ELDTUD. The individual-based approach used in this study provided precise estimates of ELDTUD and also facilitated the partitioning of variation in ELDTUD of larvae produced by the same female and among females spawning at different times and different environmental conditions.

Résumé : Chez les poissons migrateurs comme l'esturgeon jaune (*Acipenser fulvescens*), la période qui commence à la ponte des œufs, comprend les développements embryonnaire et larvaire et s'étend jusqu'à la dispersion (ELDTUD) contribue considérablement à la variation de la survie pendant toute la vie au niveau individuel et au recrutement au niveau de la population. Nous examinons l'importance relative des variables environnementales des cours d'eau (par ex., température et débit) et des effets maternels, en particulier la taille corporelle, le moment de la fraie et la position dans le milieu, sur l'ELDTUD chez des individus dont l'ascendance a été déterminée par des méthodes génétiques. Pendant la saison de reproduction de 2007, nous avons capturé des esturgeons jaunes adultes (n = 208) frayant dans l'Upper Black River (Michigan, É.-U.), ainsi que des larves (n = 1444) qui se dispersaient vers l'aval. Des modèles mixtes généralisés et l'inférence multimodèle basée sur les critères de Kullback–Leibler fondés sur la théorie de l'information nous ont permis de démontrer que tant les variables du milieu que les effets maternels reliés à la femelle et le moment de la fraie sont de bonnes variables prédictives d'ELDTUD. La diminution de l'ELDTUD au cours de la saison s'explique par un accroissement linéaire de la température et d'une réduction non linéaire du débit de la rivière. Le moment de la fraie et les femelles individuelles expliquent une forte proportion de la variation de l'ELDTUD. L'approche basée sur l'individu utilisée dans notre étude fournit des estimations précises de l'ELDTUD et facilite la répartition de la variation de l'ELDTUD entre les larves produites par une même femelle et entre les femelles frayant à divers moments et dans des conditions différentes du milieu.

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Introduction

Estimating the timing of development and of transitions between ontogenic events during early life stages and determining the relative importance of factors effecting developmental time under natural conditions are important subjects in fish biology. Embryonic and larval developmental time until dispersal (ELDTUD) is a critical period that exposes larvae to high risks of mortality due to biotic (e.g., predation and competition; Garvey et al. 1994; Paradis et al. 1996), and abiotic factors (e.g., temperature, oxygen; Chandler and Bjornn 1988; Einum and Fleming 2000). ELDTUD may vary as a function of environmental factors (e.g., temperature, stream discharge, etc.) and maternal effects (e.g., egg size) (Gillooly et al. 2002; Kamler 2002; O'Connor et al. 2007). Environmental conditions during embryonic and larval development are typically selected by parents (Trippel et al. 1997; Kamler 2002; Jørgensen et al. 2008). Therefore, maternal effects, which occur when female phenotype or environments experienced at the time and location of spawning influence offspring phenotypic traits (Mousseau and Fox 1998), and together with environmental variables associated with spawning time and spawning location can collectively contribute to embryonic and larval developmental time (Einum and Fleming 2000; Kamler 2002) and dispersal (e.g., in aquatic invertebrates, Reitzel et al. 2004; in fish, Edwards et al. 2007).

Water temperature and stream discharge are two environmental factors that play an important role in the timing of larval hatch and dispersal (Heggberget 1988; Pepin et al. 1997; Tetzlaff et al. 2005) and thus ELDTUD. Metabolic rate increases with temperature (Gillooly et al. 2001), which decreases the time required for incubation and yolk absorption. Temperature-dependent developmental time has been reported in a variety of taxa including insects (Pritchard et al. 1996; Johnson et al. 2007; Arbab et al. 2008), fish and invertebrates (Gillooly et al. 2002; O'Connor et al. 2007), and amphibians (Gillooly et al. 2002). River discharge indirectly influences developmental time via oxygen supply (Kamler 2002), and directly affects dispersal time by changing drifting and swimming speeds of larvae (Elliott 1987; Fausch et al. 2001; Siegel et al. 2003).

ELDTUD may also vary owing to maternal effects including spawning time and location, and effects associated with female body size or age. Spawning at specific times and locations has been shown to dictate conditions for offspring development and survival (Trippel et al. 1997; Jørgensen et al. 2008). Empirical and modeling studies have shown that adult spawning time and location also affect timing of larval emergence and dispersal (Einum and Fleming 2000; Reitzel et al. 2004; Edwards et al. 2007). Maternal effects on egg size, where larger females usually produce larger eggs, have been observed in fish (Chambers and Leggett 1996; Heath et al. 1999; Heins et al. 2004). Larger eggs may require longer time for embryonic development (Pepin et al. 1997; Gillooly and Dodson 2000). In addition, for many species, genetic differences among adult groups spawning at different times (isolation by time) may contribute to variation in phenotypic traits of offspring (review in Hendry and Day 2005).

Studies that simultaneously evaluate environmental and maternal effects may better explain variation in ELDTUD than studies that focus on effects of one set of variables alone. There is a lack of research that simultaneously quantifies effects of environmental factors and maternal effects on ELDTUD at the individual-level under natural conditions. Reasons for the lack of data include difficulties in identifying genealogical relationships between adults and larvae, and the need to collect a large number of parents and offspring from natural populations. The problem can be overcome using genetic makers to genetically determine parentage (Garant and Kruuk 2005; Pemberton 2008) of a population reproducing in natural and accessible habitats.

In this study, we used genetically determined parentage to examine effects of environmental factors and maternal effects on ELDTUD in a threatened fish species, the lake sturgeon (*Acipenser fulvescens*). Lake sturgeon exhibit an aggregate mating behavior where eggs and sperm are released by spawning adults over rock and gravel without nest preparation or parental care (Bruch and Binkowski 2002). Because of the species mating behavior and exposure of eggs and post-hatch larvae to environmental conditions, larval lake sturgeon experience extremely high mortality early in life (Kempinger 1988; Forsythe 2010). Therefore, selection of spawning times and locations, which determines environmental conditions that affect eggs and larvae (Mousseau and Fox 1998), by adult lake sturgeon could play important roles in offspring survival and ELDTUD. Newly-hatched larvae generally remain in the stream substrate until yolk-sac reserves are depleted, and then individuals disperse downstream in the current at night (Auer and Baker 2002; Kynard and Parker 2005; Smith and King 2005). However, factors underlying variation in ELDTUD at the individual level are still unknown.

Similar to heritable spawning time observed in many salmonid species (Siitonen and Gall 1989; Gall and Neira 2004) repeatability of spawning time among adult groups in iteroparous species may have a genetic basis. Repeatability has been used as a measure of trait heritability (Boake 1989). Data collected on spawning lake sturgeon in the Black River, Michigan (USA) over 8 years (2001–2008) revealed that repeatability of spawning time for females and males who have been captured more than two occasions was high (0.56 and 0.42, respectively, Forsythe 2010). We also observed that early-spawning lake sturgeon females produced offspring that had longer incubation times, larger body size, and larger yolk-sac reserves at hatch compared with offspring of late-spawning females (Crossman 2008), which might lead to longer period from egg deposition to dispersal (ELDTUD). If groups of lake sturgeon spawning at different times are genetically differentiated and if spawning time affects ELDTUD, genetic factors could contribute to differences in ELDTUD.

The main objective of this study was to evaluate the relative importance of environmental factors (water temperature and discharge) and maternal effects (individual female as a random effect, body size, spawning time and location) and their interactions to ELDTUD of lake sturgeon under natural conditions. We also tested whether different adult groups whose offspring differed in ELDTUD were genetically differentiated. Additionally, we quantified the degree of temperature-dependence (cumulative thermal units or CTU) for ELDTUD to evaluate the practicality of this single variable as a predictor of the timing of larval dispersal for lake sturgeon.

Materials and methods

Study site

Our study was conducted in Upper Black River (UBR), the largest tributary to Black Lake, Michigan, USA (latitude 45° 43′N, longitude 84°15′W; Fig. 1*a*). The lake sturgeon population in Black Lake is isolated from other populations in adjacent lakes by dams blocking immigration and emigration from Lake Huron (Smith and King 2005). Adults spawn over a 1.5 km-section of UBR. This section can be divided into six locations of spawning activity that were used across years (Fig. 1*b*). Shallow spawning areas (~1 m deep) and low turbidity allowed most adults to be observed and captured (Crossman 2008; Forsythe 2010) and larvae dispersing from all spawning areas to be collected (Smith and King 2005).

Sample collection

Sampling for adults was conducted daily in 2007 by wading through the entire length of the stream encompassing all spawning sites one or more times per day during the entire spawning season. We captured spawning adults (143 males and 63 females) using long-handled nets. The sex of the adults was determined by extruding gametes, and all individuals were measured for mass (kg) and fork length (cm). We also recorded date and location of capture, which were assumed to be the date and location of spawning based on our observation that lake sturgeon females spent only a few days on the spawning grounds (Forsythe 2010). A dorsal fin clip (~1 cm^2) was taken for genetic analysis.

Larval sampling was conducted at night, when the vast majority of larvae dispersed (Auer and Baker 2002). The larval sampling site was about 2 km downstream from the spawning areas (Fig. 1*a*). Five D-frame larval nets were evenly spaced across the river channel (description in Smith and King 2005) and were checked hourly from 2100–0200 h. Net locations remained consistent throughout the sampling period. Sampling began 10 d after the first spawning event was observed, and continued until there were two consecutive nights with no larvae captured. Larvae were transferred to a stream-side hatchery and were reared in different tanks by sampling night (n = 31) until individuals were large enough for dorsal fin clips to be collected nonlethally. Mortality during the rearing period was recorded, and dead larvae were preserved in 95% ethanol by sampling night. In total, 1444 tissue samples from dead and surviving larvae were available for genetic analysis. Based on the estimates of stream velocity and the proportions of total stream width sampled, juveniles collected were estimated to represent approximately 13% of total larval production (Smith and King 2005).

Environmental data

Water temperature and river discharge data were collected continuously throughout the season. Water temperatures were recorded hourly using HOBO® data loggers (Onset Computer Corp.) placed at spawning areas (Fig. 1*b*). UBR discharge was predicted based on current discharge data obtained from the United States Geological Survey (USGS) gauging station on the Pigeon River, a nearby tributary of Mullet Lake, Michigan. Using UBR and Pigeon River discharge data during April–June for 50 years (1950–2000, USGS National Streamflow Information Program), we found that daily discharge of the UBR could be predicted as a linear function of daily discharge from the Pigeon River (r^2 = 0.68, $F_{[1,4056]}$ = 9355, $P < 0.001$). We used this relationship to estimate UBR daily discharge during 2007 because there were no discharge data from the UBR that year.

Genetic analysis

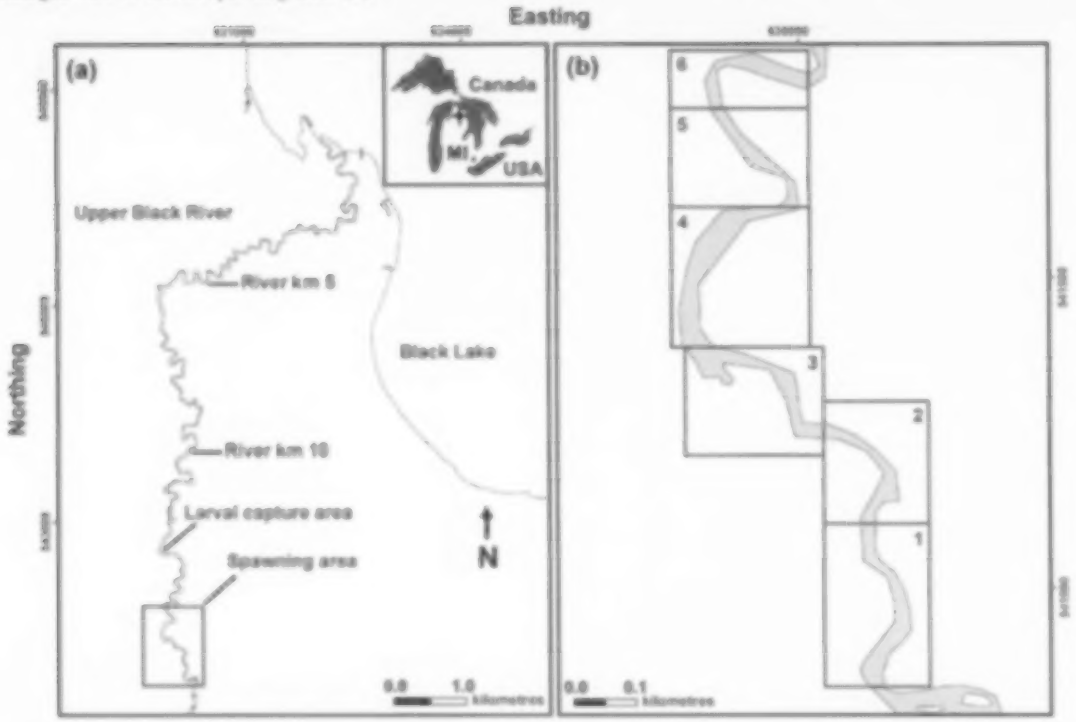
DNA was extracted from fin clips using the QIAGEN DNeasy® kit (QIAGEN, Inc.). DNA concentration was measured using a Nanodrop 1000 spectrophotometer (Thermo Fisher Scientific, Inc.). All samples were genotyped at 12 tetra-nucleotide microsatellite loci including *Spl 120* (McQuown et al. 2000); *AfuG 68B* (McQuown et al. 2002); *Aox 27* (King et al. 2001); *AfuG 68*, *AfuG 9*; *AfuG 63*, *AfuG 74*, *AfuG 112*, *AfuG 56*, *AfuG 160*, *AfuG 195*, and *AfuG 204* (Welsh et al. 2003). Using polymerase chain reaction (PCR), 100 ng DNA was amplified in 25 µL reaction mixtures containing 2.5 µL of 10X PCR buffer (1 mol·L^{-1} tris-HCl, 1.5 mol·L^{-1} $MgCl_2$, 1 mol·L^{-1} KCl, 1 g·L^{-1} gelatin, 1 mL·L^{-1} NP-40, and 1 mL·L^{-1} triton X); additions of 1 mmol·L^{-1} $MgCl_2$ (1.5 mmol·L^{-1} $MgCl_2$ for *AfuG 9*) for all reactions, but no additional $MgCl_2$ for *AfuG 63*, *Aox 27*, and *AfuG 74*; 0.8 mmol·L^{-1} deoxy-nucleotide-triphosphate (dNTP); 10 pmol fluorescently labeled forward and unlabeled reverse primers and 0.5 U of *Taq* polymerase.

All PCR reactions were conducted using a Robocyler 96 thermal cycler (Stratogene). The PCR conditions were 94 °C for 2 min, followed by 30 cycles of 1 min for primer-specific annealing temperatures (48 °C for *AfuG 9*, *AfuG 63*, and *AfuG* 112; 50 °C for *AfuG 74*; 53 °C for *Aox 27*; 56 °C for *AfuG 68* and *AfuG 68B*; 58 °C for *AfuG 56*, *AfuG 160*, and *AfuG 195*; and 62 °C for *Spl 120* and *AfuG 204*), 72 °C for 1 min, and the final extension for 2.5 min at 72 °C. PCR products were run on 6% denaturing polyacrylamide gels and visualized using a Hitachi FMBIO II scanner. Allele sizes were determined independently by two experienced personnel, based on commercially available standards (MapMarker™, Bioventures Inc.) and samples of known genotype. Errors in genotyping were empirically checked by blindly regenotyping a random 10% of all samples. Reported genotyping error is the ratio between observed number of allelic-errors and total number of alleles compared (Bonin et al. 2004).

Parentage analysis

There are numerous programs that utilize multilocus genetic data to estimate parentage (e.g., CERVUS, Kalinowski et al. 2007; PASOS, Duchesne et al. 2005; COLONY, Jones and Wang 2010), and the efficacy of use of different programs or combinations of programs has been widely debated (Christie 2010; Jones et al. 2010; Walling et al. 2010). Use of multiple programs that are based on different statistical properties to determine parentage has been advocated (Lee 2008; Jones et al. 2010). We used complimentary aspects of two programs, the Parentage Allocation of Singles on Open Systems (PASOS) program, version 1.0 (Duchesne et al. 2005) and CERVUS version 3.0 (Kalinowski et al. 2007) to conduct parentage analysis. Output of putative parent–offspring allocations from the two programs were jointly used to in-

Fig. 1. Study site on the Upper Black River, Michigan (MI), USA, showing positions of adult spawning areas and larval collection sites (*a*), and an enlarged view of the six spawning areas (*b*).



crease the proportion of offspring allocated to parents and allocation accuracy. We used PASOS to estimate the proportion of adults captured and parentage allocation correctness. PASOS can detect missing parents when they have not been collected, based on multilocus genotypes of both parents and offspring. We set the maximum number offset tolerance (MOT), the maximum number of offsets between a parental and an offspring allele that PASOS accepts as possibly due to a scoring error (Duchesne et al. 2005), of 1 and the error model (0, 0.01, 0.98, 0.01, 0) for simulations in PASOS. We conducted simulations over five iterations of 1000 pseudo-offspring to estimate the allocation correctness. Under the restricted MOT (MOT of 1 is more restricted than MOT of 2), we used the allocation function in PASOS to assign each offspring to two collected parents and estimate the proportion of adults captured from the natural population. The proportion of captured adults was used to parameterize analysis in CERVUS program.

CERVUS is the most commonly used categorical parentage technique (Christie 2010; Jones et al. 2010) and assigns progeny to a particular nonexcluded parent based on likelihood scores (LOD scores obtained by taking the natural log of the ratio of likelihoods) derived from the genotypes of all offspring and parents sampled (Marshall et al. 1998; Jones and Ardren 2003; Kalinowski et al. 2007). Simulations conducted within CERVUS to determine power and likelihood of assignment were based on empirical estimates of population allele frequency, the proportion of adults captured (PASOS output) and an empirical estimate of genotyping error (1.04%). Most likely candidate parent pairs of offspring from the assignment output were accepted as "true parent pairs" based on the criteria of ≥65% trio confidence with zero or 1 mismatch between parents and offspring genotypes. Assignment outputs from the two programs based on criteria above were then compared. Each male parent-female parent-offspring triplet that was inconsistent between the two programs was evaluated based on biological information (*e.g.*, proximity of captured time and captured location of both parents).

Genetic differences and relatedness among spawning groups

Repeatability in spawning time and spawning location for individual lake sturgeon males and females that have been captured 2 or more times (Forsythe 2010) suggests the possibility of genetic differentiation among spawning groups within the UBR population, which may contribute to differences in ELDTUD. Owing to higher repeatability in individual spawning time than in spawning location (0.56 and 0.42 vs. 0.16 and 0.04 for females and males, respectively, Forsythe 2010), we predicted that genetic differences could be detectable among members of different adult groups spawning at different times but not among groups spawning at different locations. We first estimated genetic differentiation (F_{ST}) among the three temporal spawning groups (early, middle, and late) and among six spatial spawning groups of adults using the method of Weir and Cockerham (1984) implemented in the program FSTAT 2.9.3 (Goudet 2001 (updated from Goudet 1995)). If adult groups could be genetically differentiated, we then compared distributions

and mean of inter-individual relatedness (r_{xy}) within and between genetically different groups. When a population is structured by groups of adult spawning at different times, nonrandom mating by spawning time (temporal assortative mating (Fox 2003; Devaux and Lande 2008)) can increase genetic relatedness among individuals within groups. Other authors have specifically suggested that r_{xy} is an appropriate means to quantify the degree of genetic differences between members of different groups within a population (Hendry and Day 2005). We used moment-based estimators for pair-wise relatedness, r_{xy} (Queller and Goodnight 1989) based on 12 microsatellite-locus genotypes obtained using the KIN-GROUP version 2 program (Konovalov et al. 2004). Nonparametric Kolmogorov–Smirnov tests were used to compare distributions of r_{xy} among adult groups. A permutation approach was used to test for difference in mean relatedness within and among spawning groups using a SAS-based program as in Ratnayeke et al. (2002). We also report allelic diversity, heterozygosity, probabilities of false parental exclusion, and tests (with Bonferroni correction) for deviations from Hardy–Weinberg equilibrium using CERVUS.

Statistical analysis

We defined the embryonic and larval developmental time until dispersal (ELDTUD) as the number of days elapsed between the day of female capture and the day of offspring capture as the larvae dispersed downstream from the spawning site (Fig. 1*a*). Accordingly, ELDTUD included periods of incubation, yolk absorption in the stream substrate, and migration over a distance of 2 km.

We calculated cumulative thermal units (CTU) and examined the importance of factors affecting ELDTUD. CTU (degree-day, °C) was calculated using the method of Kempinger (1988). CTU for each larva was estimated as the sum of daily temperature (adjusted by subtracting a constant 5.8 °C) during the period from egg deposition until dispersal.

We used analysis of variance (ANOVA) and pair-wise *t* tests with unequal variance to test CTU differences among offspring produced by females that spawned at different times ("early", "middle", and "late"). Females were grouped into three categories based on observed discontinuities in spawning dates among adult groups. Difference in CTU among larval groups would indicate other factors beside temperature affecting ELDTUD (Kamler 2002).

We used generalized linear and nonlinear mixed effect models to simultaneously examine environmental factors and maternal effects affecting ELDTUD. Environmental factors include mean daily water temperature and mean daily river discharge that larvae experienced during the period from egg deposition until capture. We defined maternal effects to include female spawning date (day of year), spawning location ($n = 6$, Fig. 1*b*) and body size (i.e., fork length) and the random effect of females. Females were treated as a random effect to account for nonindependence among offspring of the same female.

We initially fit data to the full model including fixed effects of water temperature (Tem_j), river discharge (Dis_i), spawning day of year (Date_m), spawning location (Loc_n), fork length (Len_o), and possible two-way interactions of fixed effects and random effect of females (Fem_o) using generalized linear mixed effect models. Two-way interactions of fixed effects were examined based on biological relevance as recommended by Burnham and Anderson (2002). Accordingly, the effect of female body size on ELDTUD would not be expected to vary as a function of the time or location of spawning. Therefore, we excluded interactions with female body size from the initial full model. We also tested for multicollinearity among independent variables of the model by examining the variance inflation factor (VIF) from the linear model with all fixed effects without interactions and the Pearson correlation of variable pairs (Graham 2003). There was evidence of multicollinearity between water temperature and day of year (VIF of temperature and day of year was 10.3 and 7.8, respectively; Pearson correlation, $r = 0.91$, $n = 1154$, $P < 0.001$). To isolate confounded effects of these two explanatory variables, we first assumed one variable was more explanatory of observed variance. We then replaced the less important variable by its residuals from the regression against the more important variable (Graham 1997, 2003; review in Heikkinen et al. 2006). We reasoned that day of year representing the conditions including temperature at spawning would be a more important explanatory variable than mean water temperature. The unique contribution of day of year was disassociated from the shared effects of temperature by adding temperature residuals (T.res_j) from regression of water temperature (dependent variable) against day of year (independent variable) in the full model. We evaluated normality of the data by examining residual plots of response and predicted variables. Based on the plot showing the nonlinear relationship between ELDTUD and river discharge, the quadratic term of river discharge was treated as a fixed effect and was also added to the model:

$$[1]\quad \text{ELDTUD} = \mu + \text{T.res}_j + \text{Dis}_i + \text{Dis}_i^2 + \text{Date}_m + \text{Loc}_n + \text{Len}_o + \text{Dis} \times \text{Date}_m + \text{Dis} \times \text{Loc}_n + \text{Date} \times \text{Loc}_m + \text{Fem}_o + \varepsilon_{ijkmno}$$

where μ is the overall mean, ($\times$) represents the interaction of two variables; and ε_{ijkmno} is the residual error for each larva. In the above model, the random effect of females (Fem_o) was assumed to be normally distributed.

Model selection for the best model from a set of all possible combinations of environmental factors and maternal effects in eq. 1 was based on Akaike Information Criterion (AIC) (Burnham and Anderson 2002). The inclusion of females as a random effect in the full model was examined first, followed by selecting fixed effects of interactions and main effects (Ngo and Brand 1997). The random effect was included if the AIC difference (ΔAIC) of the full model without and with random effect of females was greater than 4, indicating the model without random effect was less supported by the data (Burnham and Anderson 2002). We used restricted maximum likelihood (REML) to fit models differing by the presence of the random effect and maximum likelihood (ML) for competing models differing in fixed effects (Pinheiro and Bates 2000). The relative importance of environmental factors or maternal effects in ELDTUD was assessed based on ΔAIC [Δ_i = (AIC of the ith model) – (smallest AIC)] and Akaike weights ($w_i = \exp(-\Delta_i/2)$). Variables with higher sum w_i (importance weight) from all models containing the variables in question are more important

(Burnham and Anderson 2002). We also used a confidence set for Kullback–Leibler best models (Burnham and Anderson 2002) to provide the best explanation of variation in ELDTUD. The 95% confidence set represents the subset of models with the sum of $w_i \geq 0.95$. All statistical analyses were conducted using R (R Development Core Team 2009).

Results

Adult capture, larval collection, and parentage analysis

The 2007 spawning season extended from 23 April to 1 June. Timing of spawning activity was multimodal with three distinct peaks in spawning (Fig. 2*a*). More individuals were observed spawning at the beginning ("early" adults, $n = 108$ individuals) and middle of May ("middle" adults, $n = 74$) as opposed to later in May ("late" adults, $n = 24$). Larvae dispersed in two peaks 15–20 d following adult spawning (Fig. 2*b*). Water temperatures increased throughout the spawning season, from 10.6 °C to 22 °C. River discharge (range 5.71–9.61 $m^3 \cdot s^{-1}$) was higher and more variable during adult spawning than during the larval dispersal period.

Estimates of allele diversity (range from 2 to 11, average 5.3 alleles per locus) and expected heterozygosity (0.59) of lake sturgeon adults were moderate. Genotype frequencies from 11 of 12 loci conformed to Hardy–Weinberg expectations for all adults sampled. Mean polymorphic information content and nonexclusion probability for parental pairs over all 12 loci were 0.53 and 0.00006, respectively.

Of the total number of captured adults (143 males and 63 females) PASOS estimated that 89.2% of females and 87.2% of males contributed to the larvae collected. The assignment rate of offspring to two collected parents was 74.7% (1079 parents–offspring allocations) and mean allocation correctness (±SD) was estimated to be 79.1 ± 0.6%. The assignment rate from CERVUS was 85.5% (1234 allocations). Comparison of parent–offspring triplets assigned from the two programs revealed assignment consistency to be 78.6%. Exclusion of larvae with allocation discrepancies between the two programs did not affect results (data not shown). Each parent–offspring triplet in PASOS parental allocations was also one of the most likely triplets with positive LOD scores found in CERVUS. Based on concordant assignments from both programs, 1154 offspring (79.9% of larvae collected) were assigned to collected parents including 137 male parents (94.5% of males captured) and 58 female parents (92.1% of females captured). The average number of offspring collected per male was 8.4 ± 6.5 and per female was 19.9 ± 14.3.

Embryonic and larval developmental time until dispersal

ELDTUD varied from 4–36 days (mean ± SD = 20.3 ± 5.7, $n = 1154$). ELDTUD of larvae from the same female parent (the time period from the first to the last offspring collected) was 11.6 ± 4.0 d ($n = 58$ female parents). ELDTUD was significantly different among larvae whose female parents spawned during different segments (early, middle, or late) of the breeding season ($F_{[2,56.3]} = 655$, $P < 0.001$) (Table 1). Cumulative thermal units (CTU) averaged 201 ± 53 degree-days and also differed among larval groups (Table 1).

Certain combinations of both environmental variables and maternal effects better explained variability in ELDTUD than did variables within only one or the other of the variable categories (Table 2). ELDTUD was best explained by model 8 ($w_i = 0.66$; Table 2) including the random effect of females and fixed effects of temperature residuals, river discharge, quadratic effect of discharge, spawning date, spawning location, and the discharge and spawning date interaction. Fixed effects in the model explained most of variation in ELDTUD (88.0%). Of the remaining variation unexplained by the fixed effects, the random effect representing differences among females (variance 8.77, CI = 6.05–12.71) accounted for 94.5% (CI = 92.8%–95.8%), which is much greater than differences within females (i.e., residual variance) in average ELDTUD.

Based on Kullback–Leibler criteria, river discharge and spawning date associated with temperature were equally important predictors of ELDTUD. Importance weights for all of these factors (sum of w_i for models containing these factors) were close to 1 (Table 2). ELDTUD was nonlinearly related to river discharge. Coefficient estimates of the linear term (slope ± SE = –143 ± 3.0) and quadratic term (slope ± SE = 2.58 ± 0.16) of river discharge in the final model (Table 3) indicate the nonlinear decrease in ELDTUD with increasing river discharge. Larvae produced by females spawning early in the season when water temperature was comparatively low (14–15 °C) dispersed after longer periods of time compared with larvae produced by females spawning later in the year (slope ± SE = –6.40 ± 0.12, $t_{[1,56]} = -51.9$, $P < 0.001$). However, the magnitude of effects of spawning date and river discharge on ELDTUD depended on the interaction between these variables (Table 3). Spawning date effects on ELDTUD included the effect of water temperature (Pearson correlation, $r = 0.91$, $n = 1154$, $P < 0.001$). Spawning date alone explained 55.8% of the variation in ELDTUD, compared with 20.9% variation explained by water temperature (based on coefficient of determination, r^2, from linear models of ELDTUD with each predictor of spawning date and temperature, respectively). Nevertheless, temperature residuals increased model fit. The full model with temperature residuals had an AIC score lower compared with the same model without temperature residuals (ΔAIC = 6), indicating the importance of temperature when its effect was disassociated from the shared effect of spawning date on ELDTUD.

Spawning location and female body size were less important predictors of ELDTUD (importance weights were 0.30 and 0.15, respectively; Table 2). When the fixed effect of spawning date and random effect of females were included in the model to account for variation in ELDTUD of larvae from different families, the effects of spawning location and female body size on ELDTUD no longer improved model predicting (comparing AIC values of models 9 and 10, Table 2).

The confidence set for Kullback–Leibler best models included models 8, 7, and 5 (sum $w_i = 0.95$). These nested models supported the hypothesis that a combination of environmental factors and maternal effects best explained variation in ELDTUD. There was no evidence ($w_i \sim 0$) supporting the hypotheses that either environmental factors or reproductive variables alone provided the best prediction of ELDTUD of lake sturgeon.

Genetic differences and relatedness among spawning groups

Genetic differences (F_{ST}) were not significant among females and adult groups spawning at different locations

Fig. 2. (*a*) Number of adults captured and (*b*) number of larvae collected and those assigned to early, middle, or late female groups, together with mean daily water temperature and river discharge during the periods from egg deposition through embryonic and larval development until dispersal (ELDTUD).

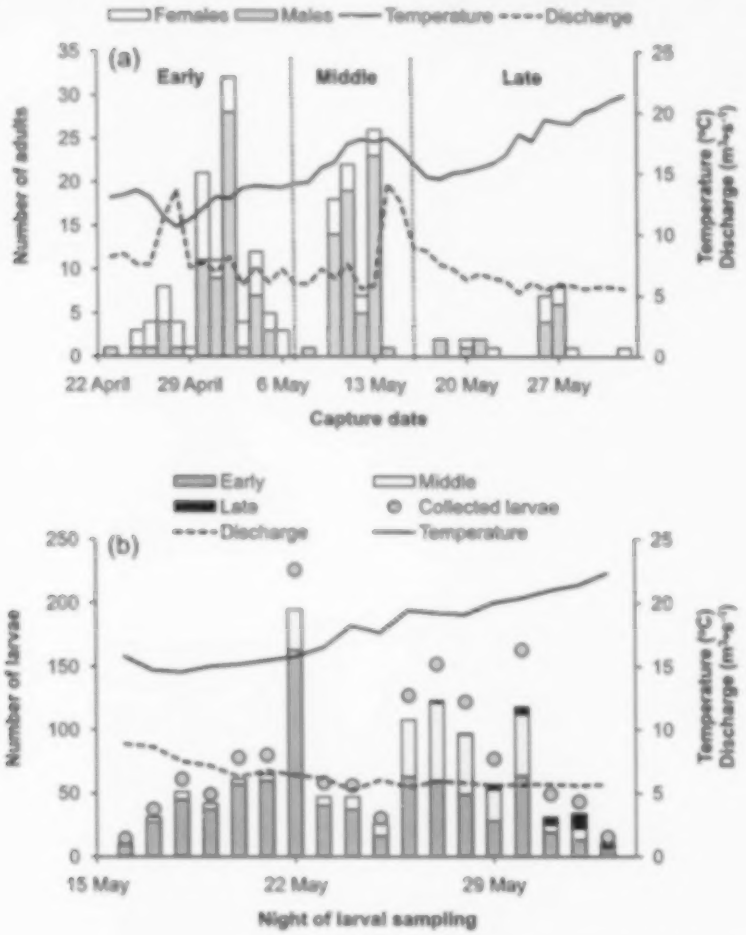


Table 1. Mean (±1 SD) temperature at spawning and daily temperature over the embryonic and larval developmental time until dispersal (ELDTUD) and cumulative thermal units (CTU) of three larval groups illustrated in Fig. 3.

Larval group (female spawning date)	No. of observations	Spawning temperature (°C)	Mean daily temperature (°C)	ELDTUD (days)	CTU (degree-days)
Early (25 April – 6 May)	792	12.9±1.0	15.4±0.5	22.7±4.6	219±48
Middle (10–13 May)	329	16.9±0.8	16.6±0.3	15.4±3.4	168±41
Late (20–27 May)	33	15.9±1.3	18.3±0.7	9.2±2.7	114±33

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. All variables differed significantly among periods ($P < 0.001$).

(95% confidence interval of overall F_{ST} (bootstrapping over loci) for only females ranged from 0.000 to 0.016, and for all adults from 0.000 to 0.002). Genetic differences were observed among adult groups (males and females) spawning at different times but not among different spawning groups of females. Pairwise F_{ST} between early and middle adults groups (0.007) was significant ($\alpha = 0.05$, after standard Bonferroni corrections, P-value adjusted = 0.016). However, no genetic differences were observed between early–late (F_{ST} = 0.002) and middle–late ($F_{ST} = 0.006$) adult groups ($P = 0.17$ and 0.20, respectively). Mean interindividual relatedness (r_{xy}) among adults of the middle spawning group (mean ± SD; 0.034 ± 0.213) was significantly higher than r_{xy} among members of the early spawning group (–0.015 ± 0.223) and late spawning group (–0.017 ± 0.209). Distributions of cumulative expected frequencies of r_{xy} values were significantly different between middle adult group compared with early and late groups (differences in distribution, Kolmogorov–Smirnov tests, 9.8% and 12.1%, respectively, $P < 0.001$). No differences in mean ($P = 0.45$) and distribution ($P = 0.81$) of

Table 2. Model structure describing embryonic and larval developmental time until dispersal (ELDTUD) and model selection criteria based on Akaike Information Criterion (AIC), AIC difference (ΔAIC), and Akaike weight (w_i).

No.	ELDTUD Model	k	AIC	ΔAIC	w_i
	Including environmental and maternal effects				
1	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + Len_r + DiscDate_{im} + DiscLoc_{in} + DatexLoc_{mn} + Fem_s$	24	2868	27	0.00
2	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + Len_r + DiscDate_{im} + DiscLoc_{in} + DatexLoc_{mn}$	23	4678	1837	0.00
3	$T.res_{ij} + Dis_i + Date_m + Loc_n + Len_r + DiscDate_{im} + DiscLoc_{in} + DatexLoc_{mn} + Fem_s$	23	361	220	0.00
4	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + Len_r + DiscDate_{im} + DatexLoc_{mn} + Fem_s$	19	2848	7	0.02
5	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + Len_r + DiscDate_{im} + Fem_s$	14	2844	3	0.15
6	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + Len_r + Fem_s$	13	3980	1139	0.00
7	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + Loc_n + DiscDate_{im} + Fem_s$	13	2844	3	0.15
8	$T.res_{ij} + Dis_i + Dis^2_i + Date_m + DiscDate_{im} + Fem_s$	8	2841	0	0.66
9	$Dis_i + Dis^2_i + Date_m + DiscDate_{im} + Fem_s$	7	2847	6	0.03
	Including only maternal effects				
10	$Date_m + Loc_n + Len_r + DatexLoc_{mn} + Fem_s$	15	6249	3408	0.00
11	$Date_m + Fem_s$	4	6232	3391	0.00
	Including only environmental variables				
12	$Tem_{ij} + Dis_i + Dis^2_i + TemxDis_{if}$	6	6310	3469	0.00
13	$Tem_{ij} + Dis_i + TemxDis_{if}$	5	6309	3468	0.00

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. Models include different combinations of fixed effects of temperature residuals ($T.res_{ij}$, from temperature [Tem_{ij}] regression against spawning day of year [$Date_m$]), river discharge (Dis_i), location (Loc_n), Fork length (Len_r), and interactions of discharge – day of year ($DiscDate_{im}$), discharge–location ($DiscLoc_{in}$), and day of year – location ($DatexLoc_{mn}$), and random effect of females (Fem_s); k, total number of parameters including intercept and error terms. Models 1 and 2 were fit by restricted maximum likelihood (REML) for testing the importance of random effect.

Table 3. Coefficient estimates of fixed effects in the best model (model 8 in Table 2) representing relationships between model parameters and embryonic and larval developmental time until dispersal (ELDTUD).

Parameters	Coefficient estimate	SE	denDF	t value	P value
Intercept	1072	18.60	1092	57.60	<0.001
Temperature residual	–0.43	0.16	1092	–2.62	<0.010
Discharge	–143	3.00	1092	–48.10	<0.001
Discharge^2	2.58	0.16	1092	16.06	<0.001
Spawning date	–6.40	0.12	56	–51.87	<0.001
Discharge×spawning date	0.72	0.02	1092	44.08	<0.001

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. SE, standard error; denDF, denominator degrees of freedom. The numerator degrees of freedom for all parameters are equal to 1.

r_{ij} were observed between early and late groups. Mean r_{ij} estimated within and between groups of adults were also not significantly different ($P = 0.08$).

Discussion

The individual-based approach used in the present study revealed that environmental and maternal factors were relatively important to ELDTUD, and that variation in ELDTUD was lower among larvae produced by the same female relative to those produced by different females. Similarly, variation in ELDTUD was lower among larvae produced by females spawning within the same group relative to those produced by females that spawned at different times (early, middle, or late) of the spawning season.

Nongenetic components of maternal effects (e.g., spawning time and spawning location) confounded by environmental factors affected ELDTUD. Using statistical approaches to account for correlations among variables and multimodel inference based on Kullback–Leibler information (Burnham and Anderson 2002; Johnson and Omland 2004), we disassociated confounding effects due to collinearity among predictor variables. Maternal effects (individual female as a random effect and spawning date) and environmental factors (water temperature and discharge) were in the confidence set for Kullback–Leibler best models, indicating that these variables were of comparable importance to ELDTUD of larval lake sturgeon.

Temperatures during spawning and embryonic and larval development can affect offspring traits, including body size (Fox and Czesak 2000) and developmental time (Gillooly and Dodson 2000; Stillwell and Fox 2005). Although temperature impacts larval developmental time in many species (e.g., Gillooly et al. 2001; O'Connor et al. 2007), interindividual variation in developmental time may be substantial. In our study, mean daily temperature only explained 20.9% of variation in ELDTUD of larval lake sturgeon. The degree of temperature-dependency of ELDTUD could differ during the three consecutive developmental periods represented by this composite variable including (*i*) embryonic development,

(*ii*) yolk sac absorption, and (*iii*) emergence and dispersal from spawning areas. The first two periods are likely more dependent on water temperature (i.e., Wang et al. 1985; Pepin et al. 1997; Kamler 2002). The third period may depend more on other environmental factors (e.g., river discharge, food, and predators), larval age or size (Elliott 1987; Day and Rowe 2002), larval behavior (Shanks 2009), lunar cycle effects on larval concealment (Hernandez-Leon 2008), and female spawning behavior (Copp et al. 2002; Hogan and Mora 2005; Shanks 2009).

Another environmental factor, river discharge, has been shown to affect the timing of larval emergence (Fausch et al. 2001) and movements (Elliott 1987; Siegel et al. 2003), and therefore was predicted to affect ELDTUD. Fausch et al. (2001) found that emergence of rainbow trout (*Oncorhynchus mykiss*) fry occurred during the period of high water velocity. After emergence, larvae can be dislodged from substrate by strong currents (salmonids, Elliott 1987; pallid sturgeon *Scaphirhynchus albus*, Kynard et al. 2007). However, for some species such as reef fishes, larvae can actively adjust their swimming speed. At high river discharge, larvae swim more slowly (Hogan and Mora 2005). Similarly, lake sturgeon larvae might exhibit considerable behavioral plasticity by remaining in substrates longer during times of high river discharge.

The effect of female spawning date on ELDTUD could be due to differences in environmental conditions (e.g., water temperature and discharge) at spawning and also to differences among adult groups. In many fish species, adult groups spawning early or late in the season might differ in maternal effects (Chambers 1997; Einum and Fleming 2000). This is also the case for lake sturgeon, evidenced by highly significant differences in ELDTUD among the three larval groups (Fig. 3) and greater among-female than within female variation in ELDTUD (Fig. 4). Adult groups that spawned at different times exhibited the low levels of genetic differentiation, providing a certain degree of support for the hypothesis that maternal effects on ELDTUD could be due in part to genetic factors. Higher F_{ST} among temporal spawning groups than spatial spawning groups is consistent with stronger effects of spawning time compared with spawning location on ELDTUD, which provides further evidence of a genetic component that may partly contribute to differences in ELDTUD. However, given the low intergroup variance in frequency of alleles at the microsatellite loci used, gene flow among members of different spawning groups is likely. Further investigation of the concordance among measures of intergroup variance in additive and neutral genetic traits is warranted.

The importance of spawning date in determining larval developmental and dispersal time observed in lake sturgeon was also reported in marine fish and invertebrates (Reitzel et al. 2004). Edwards et al. (2007) used 2-dimensional dispersal kernels to examine factors affecting larval dispersal, and found that spawning time and location might be more important than larval behavior in determining larval dispersal time. In our study, the effect of spawning location on larval dispersal time was less important than spawning date. The relatively small spawning areas of the lake sturgeon population covering 1.5 km of UBR may explain comparatively minor effects of spawning locations on ELDTUD.

Incorporating both ecological and genetic data in this study provided a useful tool to explore degrees of, and factors contributing to interindividual variation in ELDTUD of lake sturgeon. Individual-level measurement of ELDTUD based on the knowledge of parentage was more informative compared with population-based observations. For example, our results of CTU influences on ELDTUD were different from those reported by Smith and King (2005) for the same lake sturgeon population. Smith and King (2005) calculated CTU based on observations from the day of adult spawning to the day of peak larval drift. They reported that CTU for two or three larval groups from each spawning season from the years 2000 through 2002 ranged from 136.2–181.2. In their study, CTU and time to dispersal of the early larval group were lower than for the late larval group in the same year, which is opposite of our findings. Water temperature is generally colder early in the spawning season. Consequently, the time from egg deposition to dispersal of larvae would be expected to be longer, owing to temperature-dependent development (O'Connor et al. 2007). Importantly, population-based approaches could not detect important relationships between developmental time at early life stages and spawning

Fig. 3. Embryonic and larval developmental time until dispersal (ELDTUD) of three groups of larvae whose maternal parents spawned during "early" (open circle), "middle" (open diamond), or "late" (open triangle) periods of the spawning season. Where symbols appear darker, this is because more than one offspring was characterized by the same ELDTUD and female spawning date.

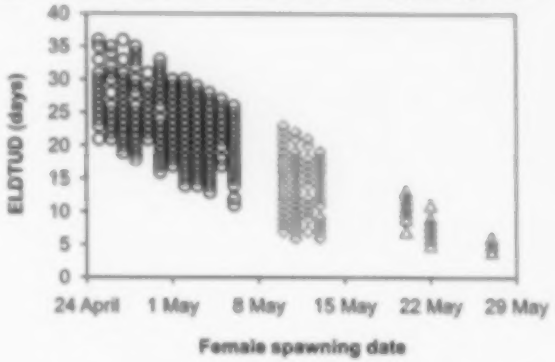
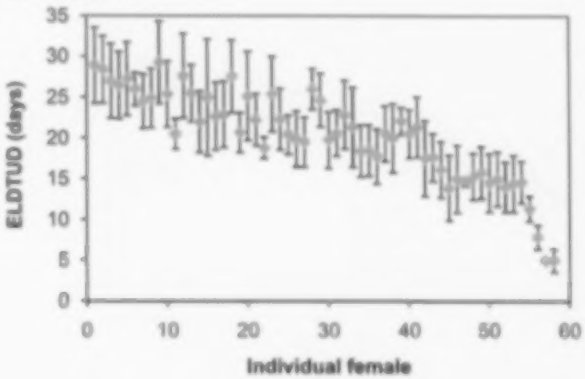


Fig. 4. Mean and standard deviation of embryonic and larval developmental time until dispersal (ELDTUD) among siblings from the same female parent. Individual females were ordered left to right by spawning date.



behavior of individual female parents. Population-based estimates of CTU might introduce considerable bias in estimating ELDTUD in the absence of genetic data that conclusively ties larvae to a specific date and location of a spawning event.

Several factors should be considered when interpreting the data. First, the characterizations of spawning time and spawning locations were based on the time and location of adult capture. This assumption could lead to decreased precision in calculating ELDTUD. However, daily surveys of the spawning sites suggest that few females spent more than 2 or 3 days in the spawning areas (Forsythe 2010), indicating minor effects on ELDTUD given the duration of spawning activity. Second, data were collected from a single year, while interannual variation in environmental conditions can be large and different groups of adults spawn in different years (Forsythe 2010). Based on Akaike weights of the best model set, we believe that the relative importance of the variables in our model will not vary substantially, although ELDTUD observed as a function of these variables may vary depending on interannual variation in environmental conditions realized each spawning season. Finally, the dispersing larvae were collected within 2 km of the spawning area, and numbers captured during this critical life stage may not reflect the numbers of larvae that disperse over different ELDTUD periods and survive.

Future research into the costs of timing of dispersal is necessary, and can be accommodated using the genetic methodologies employed in this study. Rates of mortality may vary as a function of larval body size, whereby selection acts to select individuals that disperse at different times and concomitantly at different sizes (Sogard 1997). Predation acting on different size classes of juveniles is likely a significant source of mortality (e.g., Mittelbach and Persson 1998). Spatially complex rearing habitats are expected to contribute to variation in larval growth and dispersal time. Costs of dispersal are expected to be high, and can increase if larvae disperse at certain times or developmental stages in response to stream conditions. Further analyses are warranted to address the costs of dispersal time in terms of probability of mortality during this period.

Our findings have important implications for early life history studies and for species of conservation concern. CTU and timing of adult spawning events should be simultaneously taken into account when predicting larval ELDTUD. Individual-based estimates revealed different levels of variation in ELDTUD within and between female families and among female groups. Such variation likely provides conditions for natural selection to act, and may be of importance for retention of levels of viability at the population level. Effects of environmental factors did not outweigh maternal effects including spawning time on ELDTUD. Accordingly, we suggest that the maternal effects may counter the effects of the environmental variables on development, performance, and survival of larval lake sturgeon as well as other fish species.

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Do juvenile Atlantic salmon (*Salmo salar*) use chemosensory cues to detect and avoid risky habitats in the wild?

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Abstract: We examined whether juvenile Atlantic salmon (*Salmo salar*) in the wild adjust their behaviour in response to chemical cues of predator activity during a 4-week period after emergence from gravel nests. In each of seven 75 m^2 sites in Catamaran Brook, New Brunswick, Canada, we established three contiguous sections differing in perceived predator activity by releasing stream water in control sections, conspecific alarm cues in risky sections, and nothing in buffer sections in both 2006 and 2007. As predicted, the density of young-of-the-year (YOY) salmon tended to decrease in alarm cue sections, while it increased in control and buffer sections. After the 2-week manipulation in 2006, we switched treatments so that buffer sections became alarm cue sections and alarm cue sections became buffer sections for an additional 2-week period. After the switch, the number of YOY increased least in the new alarm cue sections and most in control and new buffer sections. In contrast with YOY, the density of age 1+ parr was not affected by the experimental treatments. Our results suggest that YOY salmon can use chemical alarm cues to assess the predator activity of habitats in the wild.

Résumé : Nous examinons si de jeunes saumons atlantiques (*Salmo salar*) en nature ajustent leur comportement en fonction des signaux chimiques d'activité des prédateurs durant la période de 4 semaines qui suit leur émergence des nids de gravier. Dans chacun de sept sites de 75 m^2 dans Catamaran Brook, Nouveau-Brunswick, Canada, nous avons établi trois sections contiguës qui diffèrent par la perception de l'activité prédatrice en relâchant de l'eau du cours d'eau dans les sections témoins, des signaux d'alerte de saumons dans les sections à risque et rien dans les sections tampons en 2006 et en 2007. Comme prédit, la densité des jeunes saumons de l'année (YOY) tend à diminuer dans les sections avec signaux d'alerte, tout en augmentant dans les sections témoins et tampons. Après 2 semaines de manipulations en 2006, nous avons interverti les traitements de manière à ce que les sections tampons deviennent les sections avec signaux d'alerte et que les sections avec signaux d'alerte deviennent les sections tampons pendant 2 semaines additionnelles. Après l'inversion, le nombre de YOY a augmenté le moins dans les nouvelles sections avec signaux d'alerte et le plus dans les sections témoins et les nouvelles sections tampons. Contrairement aux YOY, les tacons d'âge 1+ ne sont pas affectés par les traitements expérimentaux. Nos résultats indiquent que les saumons YOY peuvent utiliser les signaux chimiques d'alerte pour évaluer l'activité des prédateurs dans les habitats en nature.

[Traduit par la Rédaction]

Introduction

Habitat selection has a profound influence on a number of vital processes, including population regulation, species interactions, the assembly of ecological communities, and the origin and maintenance of biodiversity (Morris 2003). Given that habitats differ in growth potential and (or) risk of predation, animals should prefer the habitat that maximizes their fitness (Dill 1978). However, the best areas for foraging are often the most dangerous, forcing individuals to trade off energy gain against safety from predators when deciding where to feed (Lima and Dill 1990). In perhaps the most elegant demonstration of this trade-off, Abrahams and Dill (1989) titrated the extra energy required to induce guppies (*Poecilia reticulata*) to forage in a more dangerous patch.

Prey capable of reliably assessing predation risk at the scale of whole habitats should presumably be at a selective advantage. To assess the safety of habitats, animals in the wild rely on various sources of information, including the direct assessment of the presence or abundance of predators via visual, chemosensory, auditory, and (or) tactile cues (Lima and Dill 1990; Kelley and Magurran 2003). For example, fathead minnows (*Pimephales promelas*) avoid areas labelled with the faeces of predatory northern pike (*Esox lucius*)

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(Brown et al. 1995), and Hawaiian roof rats (i.e., black rat, *Rattus rattus*) avoid the fecal odours of their predators, the mongoose (*Herpestes javanicus auropunctatus*) and red fox (*Vulpes vulpes*) (Burwash et al. 1998).

Animals also use chemosensory cues to assess the level of immediate predation risk (Lima and Dill 1990). Chemosensory cues released from the skin of injured fish provide reliable information about current and past predation events (Smith 1992). Many freshwater fishes, including fathead minnows, avoid areas that have been recently labelled with conspecific alarm cues under laboratory and natural conditions (Mathis and Smith 1992; Chivers and Smith 1998; Brown 2003). Similarly, terrestrial invertebrates avoid areas containing dead congeners (Grostal and Dicke 1999; Dukas 2001; Nilsson and Bengtsson 2004).

Because it is often difficult to obtain reliable information about predator abundance or activity, animals can use indirect measures such as habitat features to assess predation risk (Lima and Dill 1990; Verdolin 2006). Deer mice (*Peromyscus maniculatus*) and white-throated sparrows (*Zonotrichia albicollis*) prefer feeding stations close to or containing abundant cover (Schneider 1984; Anderson 1986). Similarly, juvenile lingcod (*Ophiodon elongatus*) and winter flounder (*Pseudopleuronectes americanus*) prefer habitats with structure (rock, shell, or sea grass) compared with bare sand habitats (Petrie and Ryer 2006; Pappal et al. 2009).

In stream-dwelling salmonids, studies of habitat selection typically focus on physical variables, such as current velocity and depth, which affect foraging profitability (Girard et al. 2004; Rosenfeld and Taylor 2009). Although juvenile salmon prefer sites with an abundance of cover (Culp et al. 1996; Dolinsek et al. 2007; Venter et al. 2008), little is known about how they actually assess predator abundance or activity when selecting habitats. In the short term, juvenile salmonids exhibit antipredator behaviour when exposed to visual and (or) chemical cues indicating the presence or activity of predators under laboratory and field conditions (Leduc et al. 2006; Blanchet et al. 2007; Kim et al. 2009). While the short-term benefits associated with antipredator behaviour are clear, it is unknown whether and how juvenile Atlantic salmon (*Salmo salar*) in the wild use chemical information to assess the relative predator activity of alternative habitats at larger temporal and spatial scales.

The objectives of this study were to examine (*i*) whether wild juvenile Atlantic salmon use chemical information to avoid habitats that have a higher perceived predator activity when settling in a new habitat and (*ii*) how they respond to changes in perceived predator activity after settling in a habitat and establishing a territory. Juvenile Atlantic salmon are ideal subjects for our study because they are relatively sedentary (Steingrímsson and Grant 2003; Breau et al. 2007), which allows us to manipulate the perceived predator activity of small sections of habitat while monitoring abundance during the 4 weeks after emergence from redds.

Materials and methods

Study site and species

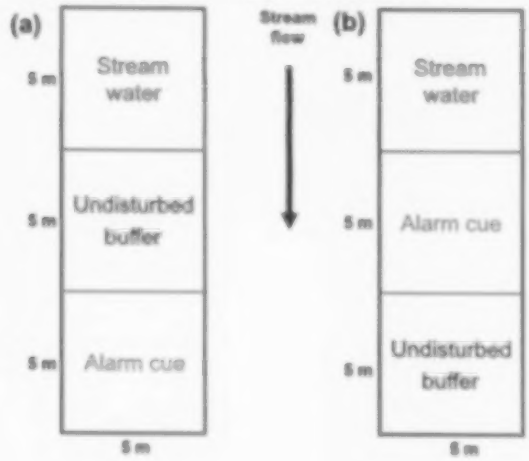
We conducted this study in the lower reach of Catamaran Brook, located in Northumberland County, New Brunswick, Canada (46°52′42″N, 66°06′00″W), from 17 June to 22 July 2006 and 21 June to 25 July 2007. Catamaran Brook is a nursery stream for a naturally reproducing population of anadromous Atlantic salmon (Cunjak et al. 1990). Young-of-the-year (YOY) Atlantic salmon emerge from gravel nests in mid-June at about 2.6 cm in fork length (Randall 1982). Upon emergence, juvenile salmon disperse from redds (gravel nests) and begin defending foraging territories, even at 2–3 cm in length (Keeley and Grant 1995).

We selected seven sites of relatively shallow depth (<50 cm) and slow current (0.2–0.5 $m \cdot s^{-1}$), which are the preferred habitats for YOY Atlantic salmon in Catamaran Brook (Girard et al. 2004). Within each site (mean width ± standard deviation (SD) = 8.18 ± 1.60 m), we manipulated the perceived activity of predators in three 5 m × 5 m sections as follows: a risky section received conspecific alarm cues; a control section received stream water; and a buffer section received nothing (Fig. 1*a*). Sections of this size (25 m^2) were chosen as an appropriate scale for our study because YOY salmon typically defend a territory of about 1 m^2 (Steingrímsson and Grant 2008) and typically move less than 5 m during their growing season (Steingrímsson and Grant 2003). Consequently, YOY salmon respond to changes in habitat quality at spatial scales as small as 6 m^2 (Dolinsek et al. 2007; Venter et al. 2008). To ensure that chemical alarm cues from the risky section had no effect on the control section (Blanchet et al. 2008), we always assigned the control to the upstream quadrat of the site (Fig. 1*a*). Furthermore, we added a buffer section between the control and risky sections so that the buffer and risky sections could be switched during late settlement (Fig. 1*b*) and fish emigrating from the risky section in an upstream direction could settle in habitat other than the control section during early settlement (Fig. 1*a*). Because there were no barriers or enclosures, each site was also exposed to the ambient risk of predation from potential predators, such as common merganser (*Mergus merganser*), belted kingfisher (*Megaceryle alcyon*), brook trout (*Salvelinus fontinalis*), and Atlantic salmon (Scott and Crossman 1973; Dolinsek et al. 2007). To minimize the potential cumulative effects of chemical alarm cues dispersing from upstream to downstream (Dionne and Dodson 2002; Kim et al. 2009), sites were at least 30 m (range: 30–93 m) apart.

To ensure that the three sections within a site were similar in habitat characteristics, we measured the depth and current velocity at 40% of the water column depth, using a Marsh–McBirney meter (model 201D, Fredericton, Maryland, USA) at five locations along a transect across each section. The depth (mean ± SD = 45.75 ± 13.43 cm) and current velocity (0.40 ± 0.27 $m \cdot s^{-1}$), the two key variables used in habitat selection (Girard et al. 2004), did not differ significantly among treatments or sites (P values all >0.18).

For the purpose of this study, we defined the early settlement period for YOY Atlantic salmon as 15 June – 7 July, the time when salmon typically emerge and disperse from their redds in Catamaran Brook (Randall 1982; Johnston 1997). During this period, YOY salmon select a suitable habitat and begin defending a territory (Armstrong and Nislow 2006). We defined the late settlement period as 8–21 July. During this late settlement period, fewer YOY Atlantic salmon emerge from redds and more fish have settled into feeding territories for the summer than during the early settlement period (Steingrímsson and Grant 2003).

Fig. 1. Experimental design in one of seven stream sites during the (*a*) early and (*b*) late settlement periods of young-of-the-year (YOY) salmon where a risky section received conspecific alarm cues; a control section received stream water; and a buffer section received nothing, twice a day for 13–17 days in 2006 and 2007.



Collection of alarm cue

Hatchery-reared Atlantic salmon parr (1+) from the Rocky Brook population of the Miramichi watershed (2006: n = 199, mean ± SD standard length = 8.57 ± 0.74 cm; 2007: n = 163, fork length = 10.64 ± 0.72 cm) were obtained from the Miramichi Salmon Conservation Centre, South Esk, New Brunswick, for use as skin donors. Skin donors were killed with a single blow on the head in accordance with Concordia Animal Care Committee Protocol AC-2005-BROW. Skin fillets from both sides were removed and immediately placed into an ice-chilled container filled with stream water. Skin fillets were homogenized and diluted with stream water. The resulting concentration (0.09 cm^2 of skin·mL^{-1}) of cue from this population elicits a consistent antipredator response in juvenile Atlantic salmon in Catamaran Brook under natural conditions (Leduc et al. 2006, 2007; Kim et al. 2009). Furthermore, alarm cues are equally effective at eliciting antipredator behaviour in field and laboratory settings for a variety of prey fishes (Brown and Godin 1999; Wisenden et al. 2004, 2010). The alarm cue was frozen in 50 mL aliquots at –20 °C until needed, whereas stream water was obtained at the site. The frozen solutions were thawed 60 min prior to use. For this study, 630 and 315 aliquots (50 mL) of alarm cue were used in 2006 and 2007, sufficient for 30 and 15 days of the experiment, respectively. The remainder of the alarm cue was used in other cognate studies.

Experimental protocol

Early settlement

We manipulated the long-term perceived predator activity in each site by releasing either the alarm cue or stream water twice a day for 17 and 15 days in 2006 and 2007, respectively (Fig. 1*a*). To coincide with the peak activity of YOY Atlantic salmon (Breau et al. 2007), we released either 50 or 100 mL of the chemical stimuli (alarm cue or stream water) at 1100 (1030–1130) and 1700 (1630–1730) for a total volume of 150 mL per day per section; the amount released in the morning was alternated each day. Studies simulating a single predation event typically use about 20 mL from 1.8 cm^2 of skin (Leduc et al. 2006; Kim et al. 2009), roughly equivalent to the size of a wound left by a predator (Smith and Lemly 1986). Hence, the release of 150 mL per section per day would be equivalent to about eight predation events, equivalent to the skin of one parr, being released in the 25 m^2 section per day. The background predation rate in Catamaran Brook is estimated to be lower than 13 predation events per section over 8 weeks if fish density is 1 YOY·m^{-2} (Girard et al. 2004). We used a 60 mL syringe to release the chemical stimuli continuously within 20 cm of the substrate while slowly walking across the site. To minimize the potential disturbance when releasing the stimulus (alarm cue or stream water), we always entered the stream upstream of the section receiving the stimulus. Hence, we walked across the stream upstream of the control section to release stream water and across the buffer section to release the alarm cue in risky sections. Furthermore, YOY Atlantic salmon do not seem to react to overhead movements, including a person walking slowly in the stream (J.-W. Kim, personal observation).

To determine how long the chemical stimulus remained in a section, we released samples of either milk or salt water (n = 3 for milk and n = 4 for salt water) in similar stream reaches (n = 7, current velocity = 0.70 m·s^{-1}, depth = 0.44 m). The initial plume of milk or salt water, detected by eye and using a conductivity meter, respectively, took an average of 11.5 s to reach 5 m downstream of the point of release. However, milk could be detected in the 5 m section for up to 20 s and the salt water for up to 34 s after release (J.-W. Kim, unpublished data).

Juvenile salmon can minimize their predation risk by either settling in alternative habitats or hiding in the substrate of risky habitats. To estimate both components of avoidance, we recorded the number, age class (only for Atlantic salmon), and species of all visible fishes in each site via snorkelling. Snorkelling is a useful technique for estimating the abundance of active fishes with a minimum of disturbance (Breau et al. 2007), particularly when electrofishing is ineffective, such as in small areas of stream or at night (Gries et al. 1997; Mullner et al. 1998; Dolinsek et al. 2007). In response to an increase in predation risk, salmon parr often become more active at night (Gries et al. 1997; Imre and Boisclair 2004; Breau et al. 2007). Hence, we estimated density during both the day and night. For all surveys, the snorkeler moved slowly upstream, completing each 1 m subsection by moving from the left bank to the right bank, taking approximately 30–40 min to complete one 15 m site during either the day or night. The daytime surveys of all sites were completed within the same day. For night surveys, we used a waterproof handheld flashlight (20 W) to illuminate fish, which were typically lethargic and unresponsive when approached. Night surveys of all sites were completed either in one or two consecutive nights.

For the initial counts, three density surveys were conducted on days 1 and 2 for each section: two during the day (between 1200 and 1600) and one at night (between 2300 and 0300). All daytime surveys were conducted at least 1 h after or before the release of the chemical stimuli at 1100 and 1700, respectively. For the final counts, we conducted

three density surveys on days 17 and 18 in 2006 and on days 14 and 15 in 2007: two during the day and one at night. We had planned to release chemical stimuli for 14 consecutive days during early settlement period. In 2006, however, heavy rain increased the water level and turbidity of all sites on day 14. Hence, to minimize any potential effects of this rainfall, we continued the treatments for a total of 17 days.

Late settlement

To investigate whether juvenile Atlantic salmon that have likely established territories respond to changes in the long-term riskiness of their local habitat, the 17-day experiment was extended for another 13 days in 2006. The treatment protocol was similar to the 17-day experiment except the buffer section during the early settlement now received the alarm cue, making it the risky section, and the risky section now received nothing, making it the buffer section (see Fig. 1*b*). We expected the density to decrease the most in the new risky sections (formerly the buffer sections), where the perceived predator activity increased the most. All sections received a total of 150 mL of chemical stimulus (alarm cue or stream water) twice daily for 13 days on 8–21 July in 2006 (Fig. 1*b*). The density survey protocol was similar to that used in early settlement.

Statistical analysis

Because YOY are primarily active in the day (Breau et al. 2007), whereas 1+ parr are active during the day and night (Imre and Boisclair 2004; Dolinsek et al. 2007), we analyzed the data separately for each age class. In addition, because of different diel activity patterns of YOY and 1+ parr, we analyzed the YOY data separately for day and night, whereas we used the average of the mean daytime densities and nighttime densities for 1+ parr. To test for the effects of perceived predator activity on the population density of YOY and 1+ parr Atlantic salmon during the early settlement periods, a repeated measures two-way analyses of variance (ANOVAs; three treatments by 2 years with the early and late settlement periods as the repeated measure and site as a block) were used to compare the mean number of salmon per section at the beginning and end of the early settlement periods. After we switched treatment in 2006, the repeated measures analysis compared the numbers at the beginning (i.e., the number at the end of the early settlement period) and end of the late settlement period.

For all analyses, only significant interactions among the effects of treatments, years, sites, and time periods were reported, unless a nonsignificant interaction among the effects of treatments, years, sites, and time periods might appear to be significant to the reader and hence require an explanation (results of all analyses are also presented in Supplemental Table S1, available online[1]). To meet the assumptions of parametric analyses, the number of YOY salmon counted during the day and night and the number of parr salmon at the start and end of the treatment during early and late settlement periods were $\log_{10}(X + 1)$-transformed. For visual purposes, all data were back-transformed following the analyses and are shown with asymmetric standard error (SE) bars.

Results

A total of 3682 fishes was counted in the 2 years, including six species: Atlantic salmon, eastern blacknose dace (*Rhinichthys atratulus*), lake chub (*Couesius plumbeus*), brook trout, white sucker (*Catostomus commersonii*), and slimy sculpin (*Cottus cognatus*). YOY Atlantic salmon were the most abundant (64.4% of all observed fishes), followed by 1+ parr Atlantic salmon (14.6%), blacknose dace (11.4%), 2+ parr Atlantic salmon (4.8%), lake chub (2.7%), brook trout (1.6%), white sucker (0.6%), and slimy sculpin (one count).

Early settlement

As expected, the final number of YOY salmon in the 75 m^2 sites after the early settlement period was higher during the day than at night (repeated measures one-way ANOVA: $F_{[1,12]} = 130.99$, $P < 0.001$; mean $\pm$ SE = 31.18 ± 4.92 for day and 1.36 ± 0.62 for night). Furthermore, the final number of YOY was higher in 2006 than in 2007 (repeated measures one-way ANOVA: $F_{[1,12]} = 20.60$, $P < 0.001$; mean $\pm$ SE = 22.75 ± 6.63 for 2006 and 9.79 ± 2.89 for 2007). Hence, we analyzed the YOY data separately for day and night.

The final number of 1+ parr salmon in the 75 m^2 sites after the early settlement period was higher in 2007 than in 2006 (repeated measures one-way ANOVA: $F_{[1,12]} = 54.71$, $P < 0.001$; mean $\pm$ SE = 2.21 ± 1.50 for 2006 and 12.43 ± 5.58 for 2007), but did not differ significantly between day and night (repeated measures one-way ANOVA: $F_{[1,12]} = 2.18$, $P = 0.17$; mean $\pm$ SE = 8.64 ± 2.00 for day and 6.00 ± 1.45 for night). Hence, for the subsequent analyses of parr, we used the average of the mean daytime and nighttime densities.

As expected, the number of YOY salmon counted during the day increased over the early settlement period (repeated measures two-way ANOVA, with site as block: $F_{[1,30]} = 40.04$, $P < 0.001$; Fig. 2*a*). As predicted, there was a significant interaction between the effects of treatments and the time periods on the number of YOY salmon counted during the day (repeated measures two-way ANOVA, with site as block: $F_{[2,30]} = 5.12$, $P = 0.012$; Fig. 2*a*). The number of salmon in the alarm cue sections decreased in 2006 and increased the least in 2007 (Fig. 2*a*). Contrary to our expectations, however, the increase in number of YOY was greatest in the buffer sections rather than in the control sections. The effect of treatments on the number of YOY per section also appeared stronger in 2006 than in 2007; however, there was no significant interaction among the effects of treatments, years, and time periods (repeated measures two-way ANOVA, with site as block: $F_{[2,30]} = 1.76$, $P = 0.19$; Fig. 2*a*). The number of YOY counted during the day was greater in 2006 than in 2007 (repeated measures two-way ANOVA, with site as block: $F_{[1,30]} = 39.30$, $P < 0.001$; Fig. 2*a*).

Because YOY salmon were absent at night in 19 out of 21 sections in 2007, we only tested the effect of treatments on the number of YOY at night during the early settlement period in 2006. Moreover, because YOY salmon were absent at

[1]Supplementary data are available with the article through the journal Web site (http://www.nrcresearchpress.com/cjfas).

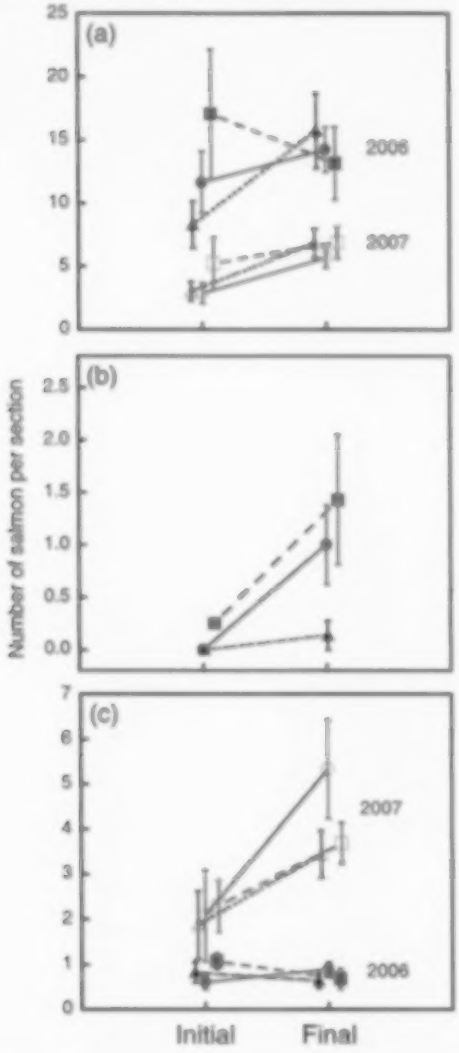


Fig. 2. Mean number (± standard error (SE), $n = 7$) of Atlantic salmon exposed to three treatments (stream water: ●, solid line; alarm cue: ■, dashed line; and a buffer: ▲, dotted line) during the early settlement period in 2006 (closed symbols) and 2007 (open symbols) for young-of-the-year (YOY) salmon (*a*) during the day and (*b*) at night and (*c*) for parr during the day and night. (Note that the results for YOY at night is reported for 2006 only.)

night in all 21 sections at the start of early settlement period in 2006, we analyzed the data using a one-way ANOVA with a randomized block design on the final number of YOY at night during early settlement. In contrast with the patterns in the daytime data, the number of YOY at night appeared to increase least in the buffer section and most in the alarm cue and control sections (Fig. 2*b*); however, this difference was not significant (one-way ANOVA, with site as block: $F_{[2,12]} = 1.84$, $P = 0.20$; Fig. 2*b*). However, the contrasting patterns between the day and night data in 2006 led to a significant interaction among the effects of treatments, time of the day, and time periods (repeated measures two-way ANOVA, with site as block: $F_{[2,30]} = 8.73$, $P = 0.001$). Hence, the treatments had opposite effects on the number of YOY during the day and at night during the early settlement period in 2006.

In contrast with YOY salmon, there was no significant interaction between the effects of treatments and the time periods on the number of 1+ parr (repeated measures two-way ANOVA, with site as block: $F_{[2,30]} = 2.31$, $P = 0.12$; Fig. 2*c*). However, there was a significant interaction between the effects of time periods and years on the number of parr (repeated measures two-way ANOVA, with site as block: $F_{[1,30]} = 17.01$, $P < 0.001$); the number of parr increased over the early settlement period in 2007 (repeated measures one-way ANOVA, with site as block: $F_{[1,12]} = 38.21$, $P < 0.001$; Fig. 2*c*), but remained the same in 2006 (repeated measures one-way ANOVA, with site as block: $F_{[1,12]} = 0.17$, $P = 0.68$; Fig. 2*c*). Furthermore, the number of parr was greater in 2007 than in 2006 (repeated measures two-way ANOVA, with site as block: $F_{[1,30]} = 73.12$, $P < 0.001$; Fig. 2*c*).

Late settlement

As expected, the number of YOY during the day increased over the 13-day late settlement period (repeated measures one-way ANOVA, with site as block: $F_{[1,12]} = 45.24$, $P < 0.001$; Fig. 3*a*), indicating that some fish were still selecting habitats in which to settle at this time. The number of YOY salmon increased significantly more in control and buffer sections than in risky sections (repeated measures one-way ANOVA, with site as block: $F_{[2,12]} = 6.26$, $P = 0.014$; Fig. 3*a*). Perhaps because of alarm cues dispersing downstream, the buffer section had an intermediate final number of YOY (Fig. 3*a*).

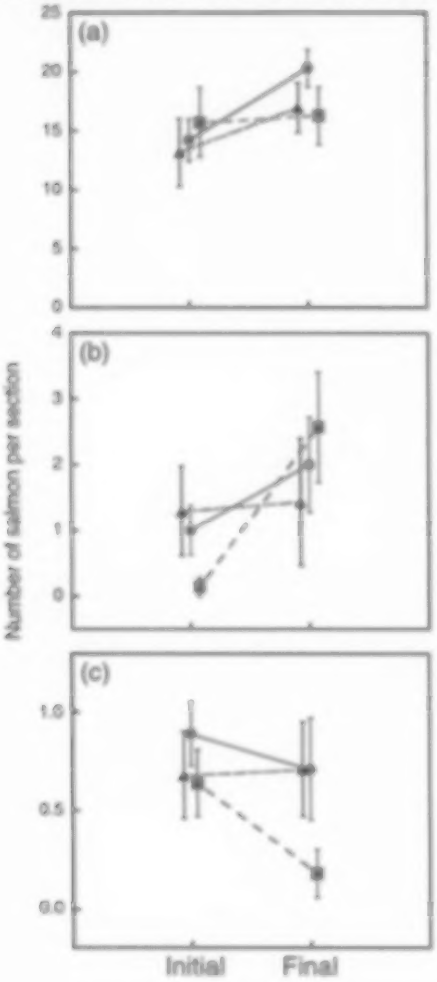
At night, the number of YOY per section increased over the 13-day late settlement period (repeated measures one-way ANOVA, with site as block: $F_{[1,12]} = 10.80$, $P = 0.007$; Fig. 3*b*), and this increase differed between treatments (interaction between treatments and time periods: $F_{[2,12]} = 5.84$, $P = 0.017$; Fig. 3*b*). Again, in contrast with the patterns during the daytime, the number of YOY salmon increased more in the risky sections than in the control or buffer sections (Figs. 3*a* and 3*b*). Hence, the treatments again had opposite effects on the number of YOY during the day and at night during the late settlement period in 2006.

Contrary to the results for YOY, the number of 1+ parr per section did not differ significantly over the 13-day late settlement period (repeated measures one-way ANOVA, with site as block: $F_{[1,12]} = 3.82$, $P = 0.074$; Fig. 3*c*). Furthermore, there was no significant interaction between the effects of the treatments and the time periods on the number of parr per section ($F_{[2,12]} = 1.70$, $P = 0.22$; Fig. 3*c*).

Discussion

Our results suggest that YOY Atlantic salmon can use chemical information to directly assess the relative activity of predators in different habitats and then avoid particularly dangerous habitats. During the early settlement period, the number of YOY during the day in risky sections decreased or increased less than that in the buffer and control sections. The magnitude of increase in density in the buffer sections

Fig. 3. Mean number (± standard error (SE), $n = 7$) of Atlantic salmon exposed to three treatments (stream water: ●, solid line; alarm cue: ■, dashed line; and a buffer: ▲, dotted line) during the late settlement period in 2006 for young-of-the-year salmon (*a*) during the day and (*b*) at night and (*c*) for parr during the day and night.



was not expected and may have been caused by fish moving upstream out of the risky sections. During the late settlement period, the number of YOY salmon increased most in the control and buffer sections and least in the risky sections, where the perceived predator activity increased the most.

It is also possible that YOY salmon remained within risky sections but altered their behaviour by spending more time hidden in the substrate (Leduc et al. 2007) and were not counted during surveys. We think this explanation of our results is unlikely for three reasons. First, the delay between the release of the stimulus and the subsequent density survey (i.e., >1 h) was much longer than the latency to resume feeding in response to the same stimulus (i.e., <50 s; Kim et al. 2009). Second, YOY salmon are most active during the day (Breau et al. 2007), so it is unlikely that the decrease in daytime density could be entirely accounted for by more YOY salmon hiding in refuges. Third, if YOY were indeed hiding in the substrate during the day, then we would have presumably detected them during night surveys. While the increase in night densities was greatest in the risky sections, the magnitude of this increase could not account for differences observed during the day. Nevertheless, we cannot rule out the alternate explanation that YOY salmon responded to the alarm cues by hiding in the substrate during the day and night. If true, this result would suggest that YOY salmon hide in the substrate much longer during the summer than previously thought (Breau et al. 2007). Taken together, these results suggest that YOY salmon detect and avoid the sites with alarm cues. Furthermore, our data suggest that alarm cues have longer-lasting effects on the behaviour of YOY salmon at larger spatial scales than is typically measured during short-term antipredator experiments (Leduc et al. 2006; Kim et al. 2009).

Following the switch of treatments in 2006, we found no significant decline in numbers in the alarm cue sections (formerly the buffer sections), suggesting that once YOY have settled on a foraging territory within a habitat, an increase in predator activity is not sufficient to cause them to relocate to "safer" habitats. Because the quality of alternative locations is uncertain, the increased energy expenditure and decreased energy intake during a relocation may decrease the net benefits of leaving risky sections (McDougall and Kramer 2007). In addition, if most YOY salmon have established their territories, then the prior residency effect (Cutts et al. 1999) may make the costs of relocation outweigh the costs of staying in risky habitats. Alternatively, YOY salmon can defend smaller territories to compensate for the increased risk (Kim 2009; Kim et al. 2011). However, the increase was less in the alarm cue than in the other treatments, suggesting that new settlers either avoided risky sites or hid in the substrate.

Interestingly, the patterns of YOY abundance at night during early and late settlement periods were significantly different from and opposite to those observed in the day; the increase in density at night was highest in the alarm cue sections and lowest in the buffer sections. The relatively few YOY found in risky habitats may become more active at night to avoid the higher perceived activity of predators during the day. Furthermore, the few fish in risky habitats may benefit from the reduced competition for food and space, which often leads to an increased growth rate (Imre et al. 2005).

Contrary to our results for YOY, 1+ parr did not respond to the experimental treatments. 1+ parr clearly detect and respond to alarm cues in the short term by decreasing their foraging rates and increasing their latency to foraging (Kim et al. 2009). Because 1+ parr already forage primarily at night (Imre and Boisclair 2004; Breau et al. 2007), they may be less influenced by the increased perceived predator activity of alarm cue sections during the day. Alternatively, 1+ parr may have reached a size that makes them less vulnerable to gape-limited fish predators such as brook trout and Atlantic salmon (Sogard 1997).

Overall, our data suggest that YOY Atlantic salmon can use chemical information to assess the quality of habitat in terms of predator activity. Our study suggests that if habitats differ markedly in ambient predator activity, YOY will avoid settling in particularly risky habitats or hide in the substrate

for long periods of time. Whether the differences in perceived predator activity between the treatments in our study represent the degree of spatial variability in actual predation risk in salmon streams is an open question, especially so given that the treatment effect was not strong enough to override the differences in initial density. While our study tested whether the differences in perceived predator activity in each section influence settling decisions, it would be important to examine how the intrinsic riskiness of habitat (Lima and Dill 1990; Verdolin 2006) influences the population density of a given habitat, potentially affecting the relative predation risk of an individual. It would also be interesting to examine whether and how predators redistribute themselves in response to the altered distribution of prey. Moreover, investigating the potential interaction between the effects of predation risk and population density on habitat selection would lead to the better understanding of population consequences at broader spatial and temporal scales (Werner and Peacor 2003; Blanchet et al. 2008). Further research is also needed to determine if YOY salmon use alarm cues to assess the spatial variation in predation risk in an unmanipulated system. Furthermore, given the well-known difficulties in studying long-term predation risk in natural populations (Lima and Steury 2005), our current study suggests that chemical alarm cues may provide a valuable tool for future studies examining the ecologically relevant effects of predation.

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Water chemistry and dissolved organic carbon trends in lakes from Canada's Atlantic Provinces: no recovery from acidification measured after 25 years of lake monitoring

Thomas A. Clair, Ian F. Dennis, and Robert Vet

Abstract: We analyzed chemistry trends for 66 Atlantic Canada lakes using data collected from 1983 to 2007, as well as from 1990 to 2007 and 2000 to 2007 for the original 66 and a further 25 lakes that were later added to the network. Though receiving the lowest acid deposition in eastern North America, the region's waters are seriously affected by acid rain because of poorly buffering soils and bedrock. Earlier work had shown that despite large decreases in sulfate deposition, lake pH and calculated acid neutralization capacity (ANC_c) had not increased as they had elsewhere in North America and Europe. Despite a 50% decrease in acid deposition, a further 10 years of lake chemistry data showed a regional increase in ANC_c only at the beginning of the sampling period but no increase since the early 1990s. There were also no increases in pH and base cations in the region's lakes. We show a regional increase in Gran titration ANC (ANC_G) from 2000 to the present, which we ascribe to increases in dissolved organic carbon that is probably due to a regional increase in annual air temperatures.

Résumé : Nous avons déterminé les tendances chimiques dans 66 lacs de la région atlantique du Canada à partir de séries données récoltées de 1983 à 2007, de 1990 à 2007, ainsi de 2000 à 2007 dans les 66 lacs d'origine, ainsi que dans 25 lacs additionnels rajoutés plus tard au réseau. Bien qu'elles reçoivent les dépôts acides les plus faibles de l'est de l'Amérique du Nord, les eaux de la région sont fortement affectées par les pluies acides à cause de la faible capacité tampon des sols et de la roche mère. Des travaux antérieurs ont montré que malgré une diminution importante des dépôts de sulfates, le pH des lacs et la capacité calculée de neutralisation des acides (ANC_c) n'ont pas augmenté comme ils l'ont fait ailleurs en Amérique du Nord et en Europe. En dépit d'une réduction de 50 % des dépôts acides, les données couvrant les 10 années subséquentes de chimie des lacs indiquent une augmentation régionale de l'ANC_c seulement au début de la période d'échantillonnage, mais aucun accroissement depuis le début des années 1990. Il n'y a pas non plus eu d'augmentation du pH et des cations basiques dans les lacs de la région. Nous démontrons une augmentation régionale de l'ANC par titrage de Gran (ANC_G) de 2000 à aujourd'hui que nous expliquons par une hausse du carbone organique dissous qui est sans doute due à une augmentation de la température annuelle de l'air dans la région.

[Traduit par la Rédaction]

Introduction

Acid precipitation caused by sulfur oxides (SO_x), which are emitted by industrial and power generating sources, has been a major concern in eastern North America, especially in regions where the geological terrain and soils contain little acid buffering capacity. North American emissions peaked in the mid-1970s (Graedel et al. 1995), though large-scale sampling for environmental effects did not begin in most regions until the early 1980s when the scope of environmental problems became most evident. Since wet deposition sampling was started in Canada in the early 1980s, measured values have decreased by approximately 50% in much of Canada (Vet et al. 2005).

The eastern-most portion of North America, Canada's Atlantic Provinces, receives acid deposition originating from the midwest and east coast of the United States as well as eastern Canada (Vet et al. 2005). The Atlantic Provinces are lightly populated, with 2.3 million inhabitants in an area encompassing 247 000 km^2. Much of the region has thin, glaciated soils that cover granite and slate bedrocks, providing little buffering capacity against acidification (Shilts 1981). Long-term acidification effects have led to surface water Gran titration alkalinity values as low as –20 mg·L^{-1} (excess acidity) and pH values ranging from 4.5 to 5.5 over large parts of the region (Clair et al. 2007). These high acidity

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Fig. 1. Location of sampling regions and lake clusters in the Atlantic Provinces. Numbers denote the location of the Canadian Air and Precipitation Monitoring Network (CAPMoN) site: 1, Harcourt; 2, Jackson; 3, Bay d'Espoir; 4, Kejimkujik. The polyhedrons show the limits of the subregions, and the dark areas show lake cluster zones.

conditions have caused severe stresses to ecosystems in the region, as Watt (1987) identified a number of rivers in Nova Scotia where Atlantic salmon (*Salmo salar*) populations have either been extirpated or severely depleted because of acid precipitation.

Since the early 1980s, Environment Canada (EC) has been monitoring atmospheric wet deposition at four Canadian Air and Precipitation Monitoring Network (CAPMoN) atmospheric sites in Atlantic Canada. EC has also been monitoring the chemistry of approximately 66 lakes in this region since the mid-1980s (the number of lakes has changed with time), with the longest records being in southwestern Nova Scotia (WNS) and the island of Newfoundland (NF) (Fig. 1). A further 25 sites were later added in eastern Nova Scotia (ENS) and southwestern New Brunswick (NB) to fill in geographical gaps.

Trend analysis has been done continually on the chemistry data of network lakes to assess the effectiveness of North American emission reductions. Using data collected from 1983 to 1994, Clair et al. (1995) showed that SO_4^{2-}, pH, base cations (C_b), and calculated acid neutralization capacity (ANC_c) of the region's lake waters initially increased as atmospheric SO_4^{2-} wet deposition decreased. In later studies (Clair et al. 2002; Stoddard et al. 1999) using data from 1983 to 1997 and to 2000, surface water chemistry trends were shown to have changed significantly, with lake SO_4^{2-}, C_b, and ANC_c all decreasing, while the low pH values in this region did not increase. A further analysis using a shorter data set collected from 1990 to 2001 (Jeffries et al. 2005) again showed decreases in atmospheric and lake SO_4^{2-}, ANC_c decreases in regional lakes, and no significant trends in lake pH or calcium. The ANC_c decrease and the lack of pH and calcium responses were initially unexpected considering the magnitude of the SO_4^{2-} wet deposition decrease.

In a more recent study, Skjelkvåle et al. (2005) compared acidified surface water chemistry trends for 12 geographical regions in western Europe and eastern North America and found that Atlantic Canada and the adjacent state of Maine, USA, was the only region where both Gran titration ANC (ANC_G) and ANC_c values were still decreasing and not responding to reduced acid deposition. However, they showed that this type of pattern had been noted before in other regions and was usually followed by later chemistry improvements. To add further confusion to interpretation, Whitfield et al. (2006) used 1983–2005 data on a nine lake subset of the EC network and showed that as SO_4^{2-} decreased, C_b and ANC_c also decreased, while pH increased.

The fact that Atlantic Canada lakes have not followed the same chemical trends as other regions showed that a better understanding of water chemistry trends from this region is needed. The purpose of this paper is therefore to reanalyze lake chemistry trends from 91 acid-sensitive lakes in Nova Scotia and the island of Newfoundland (Fig. 1), using an additional 10 years of data beyond the Stoddard et al. (1999) paper, to see if lake chemistry was finally changing to expected patterns. We also assessed trends in chloride (Cl^-), which is an important indicator of marine influence and thus storm activity in this region, as well as dissolved organic carbon (DOC), a surrogate for natural organic acidity that can affect both water pH and ANC_G, to better understand what other factors may be controlling acidification (chemical) changes.

The main null hypothesis tested was that the extension of the data series would show no trends in increasing or decreasing pH, ANC, or base cations with the known decrease in wet deposition SO_4^{2-}. The alternate view was that these acidification-related parameters would show improvements. Our analysis also discusses why results from this region have, up to now, been different from other parts of the world where there has been a better relationship between wet deposition reductions and water chemistry improvements.

Materials and methods

Study area and sampling methods

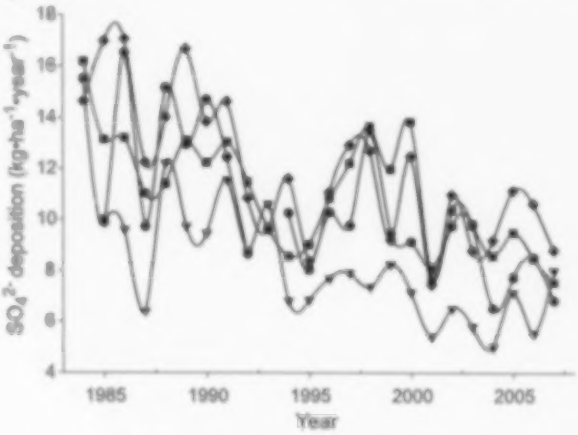
Four CAPMoN atmospheric wet deposition sampling sites (Harcourt, Jackson, Bay d'Espoir, and Kejimkujik) are located within the study region (Fig. 1). Daily wet deposition monitoring has taken place at all of these sites since the early 1980s, and daily dry deposition values have been estimated at the Kejimkujik site (only) during the same period.

The study region has been well described in previous work (e.g., Clair et al. 2007). Most of EC's acid rain monitoring lakes are located in glaciated terrain with thin soils (<2 m), usually underlain by granites or slates (Shilts 1981). Because of the region's changeable geology, as well the lakes' variable distances from continental SO_x emission sources, Atlantic Canada was divided into four subregions, each of which received different deposition amounts: WNS and NB were located in the western-most portion of the region and received the most acid deposition; ENS and NF received lower amounts (Fig. 1), as they were furthest from continental S emission sources.

Most of the WNS sites and half of the ENS are underlain by Ordovician slates and thin podsols, which provide little buffering capacity against acidification (Kerekes et al. 1982), while the other lakes in ENS are situated either on Devonian or Precambrian granites also generating thin soils and thus little acid buffering (Shilts 1981). The situation in NF is similar to that in NS with most sites being located either on granitic rock in the west or slates in the east. New Brunswick sites are underlain by Devonian mafic rocks.

As the lake monitoring network was modified over time, usually for logistical reasons, the sampling start periods varied depending on the region. Most WNS and NF sites have been sampled since 1983 or 1984, while the ENS sites and six sites in WNS were added in 1990 to provide enhanced geographical coverage of those regions. Further sampling of

Fig. 2. Sea salt corrected wet deposition SO_4^{2-} trends from the atmospheric monitoring networks. Kejimkujik (diamonds) is located in western Nova Scotia (WNS), Harcourt (circles) is near the New Brunswick (NB) cluster, Jackson (squares) is closest to eastern Nova Scotia (ENS), and Bay d'Espoir (triangles) is located in Newfoundland (NF). The curves were smoothed using a spline interpolation approach.



10 lakes was begun in NB during 2000 to further widen the sampling area. All lake sampling was conducted semiannually using a helicopter during the spring and fall overturn periods, which usually was in May and October. Samples were collected from the pontoon at 0.5 m depth, kept cool, and shipped to EC's Atlantic Laboratory for Environmental Testing (ALET). In Terra Nova National Park, sampling was done by Parks Canada staff wading out from shore and collecting samples 0.5 m from the surface.

All samples were analyzed according to ALET standard protocols (Clair et al. 2002). pH was measured potentiometrically; SO_4^{2-}, Cl^-, and NO_3^- were done by ion chromatography; while Ca^{2+}, Mg^{2+}, K^+, and Na^+ were done by atomic absorption up to 1999 and by inductively coupled plasma emission spectrometry afterwards. Quality control–assurance studies showed no differences between results before and after 1999, which could be ascribed to the methods change. ANC_G was estimated from the titration curve (μequiv.L^{-1} of HCO_3^-). Under highly acidic conditions, ANC_G can produce negative values, which we define as excess acidity. ANC_c was calculated by subtracting the sum of acid anions ($\sum C_a$ in equivalent units) from the sum of base cations ($\sum C_b$). DOC was analyzed using two methods. Before 1994, DOC was analyzed using a UV–persulfate method, which was shown to underestimate concentrations (Koprivnjak et al. 1995). After 1994, a high temperature combustion method was used, which increased mean values by approximately 20%. Clair et al. (2008) describe the need for the correction and its application for NS waters.

Most of the sites sampled had chloride (Cl^-) concentrations >3 mg·L^{-1}, which indicated that the nearby western Atlantic Ocean was contributing ions to fresh waters. To provide a more accurate picture of anthropogenic effects, the sea salt contribution was removed by assuming that all Cl^- was of marine origin and that the marine contribution of other ions (SO_4^{2-}, NO_3^-, Ca^{2+}, and Mg^{2+}) is in the same pro-

Table 1. Total precipitation and wet deposition trends ($kg \cdot ha^{-1}$) as well as significance levels (p value) at the four regional Canadian Air and

	Precipitation (cm)		H^+($kg \cdot ha^{-1}$)		SO_4^{2-}($kg \cdot ha^{-1}$)		NO_3^-($kg \cdot ha^{-1}$)		Cl^-($kg \cdot ha^{-1}$)	
	M–K	p	M–K	p	M–K	p	M–K	p	M–K	p
1984–2007										
Kejimkujik	0.992	0.32	–4.11	**0**	–3.57	**0**	–1.93	**0.05**	1.19	0.23
Harcourt	0.74	0.46	–4.00	**0**	–3.59	**0**	–1.24	0.21	1.87	*0.06*
Jackson	0.595	0.55	–3.44	**0.001**	–2.80	**0.005**	–1.09	0.28	2.15	**0.03**
Bay d'Espoir	0.536	0.59	–3.79	**0**	–3.18	**0.001**	–2.17	**0.03**	–0.14	0.89
1990–2007										
Kejimkujik	0.19	0.85	–3.48	**0.001**	–1.93	**0.05**	–1.62	0.10	1.40	0.16
Harcourt	–0.33	0.74	–3.69	**0.001**	–2.68	**0.007**	–1.98	**0.04**	0.82	0.41
Jackson	–0.34	0.73	–2.83	**0.004**	–1.78	*0.07*	–1.40	0.16	1.66	*0.09*
Bay d'Espoir	–0.79	0.43	–4.07	**0.001**	–2.99	**0.002**	–2.99	**0.002**	–0.42	0.67
2000–2007										
Kejimkujik	0.49	0.62	–0.90	0.36	–0.74	0.45	–1.73	*0.08*	0.98	0.32
Harcourt	0	1	–1.51	0.13	–0.87	0.38	–1.48	0.13	0.98	0.32
Jackson	–0.98	0.32	–1.62	0.11	–1.48	0.13	–2.22	**0.03**	0.37	0.71
Bay d'Espoir	0.24	0.80	–2.01	**0.04**	–1.24	0.21	–1.73	*0.08*	0	1

Note: Bold p values denote significant trends at >95% confidence; italic p values are significant at >90%; $p = 0$ denotes trends significant at >99.99%.

portion as that of seawater. This portion is calculated using the following formula:

$$(1) \quad ion_{\text{sea salt corrected}} = ion_{\text{total}} - (ion_{\text{total}} \cdot f)$$

where f is an ion-specific constant calculated from the seawater Cl^- : specific ion ratio (Watt et al. 1979). Trend analyses were done on both sea salt corrected and uncorrected data. However, our analyses showed no differences between them, so we report only trend analyses for the corrected data.

Statistical analysis

Long-term trends for wet deposition and lake chemistry were estimated at each site using the seasonal Mann–Kendall nonparametric trend test (Hirsch and Slack 1984; Hirsch et al. 1982) with the software MULTITEST (Grimvall 2010). Individual lake SO_4^{2-} trend Z scores were plotted for the time windows 1983–2007, 1990–2007, and 2000–2007 to get a picture of the within-region variability and the significance of trend directions for the various parameters.

The software also allowed us to assess the combined trends of parameters within each subregion to be able to provide a general statement of whether or not that whole region showed a large-scale change. The approach used the covariance sum test method developed by Lettenmaier (1988), which computes a statistic (r) based on the differences among all possible lake data pairs, thus representing the net direction of movement of the complete regional time series data. The trend significance statistic calculated using this approach (Z, also called the M–K statistic) is a measure of trend magnitude and its significance, but is not a direct quantification of the trend magnitude. To assess trend magnitude, we used a linear regression approach.

Ehrman and Clair (1995) showed that there are often short-term trend directional changes within long-term data sets in Atlantic Canada. To insure that the measured trends comparisons were relevant when comparing sites with different time series lengths, we calculated trends for three time windows depending on data availability. First, we calculated 1983–2007 trends for WNS and NF. We then calculated trends from 1990 to 2007 for WNS and NF as well as ENS. Finally, we calculated trends from 2000 to 2007 for NB as well as the other three subregions. Using this approach, we were thus in a position to assess if the shortest data series (ENS and NB) could provide a useful assessment of long-term trends for those particular regions when we compared its results with those from the other, longer data series. Our secondary null hypothesis was that both medium and short trends would provide similar trend information to that from the longer series, and thus the shorter NB and ENS results would be comparable to those from the longer WNS and NF series.

Results

Regional ion deposition

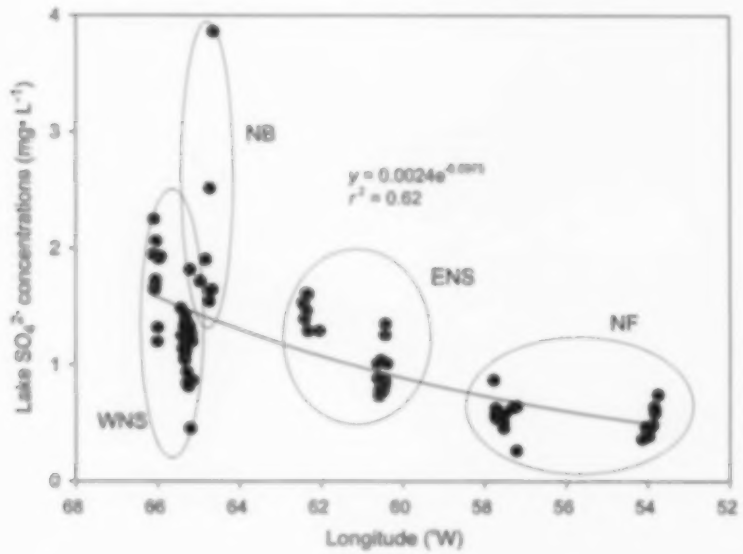
Atmospheric wet and dry deposition fluxes of sea salt corrected S and NO_3^- at Kejimkujik, NS, have been analyzed and presented in detail (Vet et al. 2005). During the period 1998–2002, the annual average sea salt corrected S deposition flux (wet plus dry) was estimated to be 5.75 $kg \cdot ha^{-1} \cdot year^{-1}$, with 72% attributable to wet deposition and 28% to dry. A source contribution analysis showed that approximately 40% of the 5.75 $kg \cdot ha^{-1} \cdot year^{-1}$ originated from the eastern seaboard region of the United States; 13% from the US Midwest and southern Ontario; 25% from Quebec, northern Ontario, and western Canada; 14% from the Atlantic Ocean; and 8% from within the Atlantic Region in general. Data analysis showed that WNS and NB are the areas closest to acid deposition originating in the eastern United States and central Canada and thus receive the greatest wet deposition amounts, while Bay d'Espoir in NF received the lowest.

The highest mean annual sea salt corrected SO_4^{2-} wet deposition during the study period 1984 to 2007 was 12.2 $kg \cdot ha^{-1} \cdot year^{-1}$ at the Kejimkujik CAPMoN site, while the lowest mean value was 8.3 $kg \cdot ha^{-1} \cdot year^{-1}$ at Bay d'Espoir, NF, a site 850 km to the east of Kejimkujik and furthest from

Precipitation Monitoring Network (CAPMoN) sites throughout the period 1984 to 2007.

NH_4^+ (kg·ha^{-1})		Ca^{2+} (kg·ha^{-1})		Mg^{2+} (kg·ha^{-1})		K^+ (kg·ha^{-1})	
M–K	*p*	M–K	*p*	M–K	*p*	M–K	*p*
1.39	0.164	0.67	0.5	1.44	0.15	1.39	0.16
0.48	0.634	0.42	0.67	0.34	0.73	0.84	0.4
2.26	**0.024**	1.09	0.28	1.74	*0.08*	2.18	**0.02**
–1.33	0.184	0.65	0.52	0	1	–1.16	0.25
1.85	*0.06*	1.89	*0.06*	1.48	0.14	2.12	**0.03**
–0.12	0.90	1.13	0.26	–0.12	0.90	0.45	0.64
1.06	0.29	1.67	*0.09*	1.14	0.26	1.63	*0.10*
–0.95	0.34	0.91	0.35	–0.95	0.34	–0.22	0.81
0.49	0.62	1.00	0.31	0.99	0.32	1.87	*0.06*
–0.49	0.62	–0.99	0.32	0.12	0.90	–0.87	0.38
–0.98	0.32	–0.74	0.45	–0.25	0.80	–0.62	0.53
–0.98	0.32	2.63	**0.02**	–0.25	0.80	0.62	0.53

Fig. 3. West–east reduction of 2000–2005 median lake SO_4^{2-} in the sampling network. The subregions lake groups are delineated in the figure.

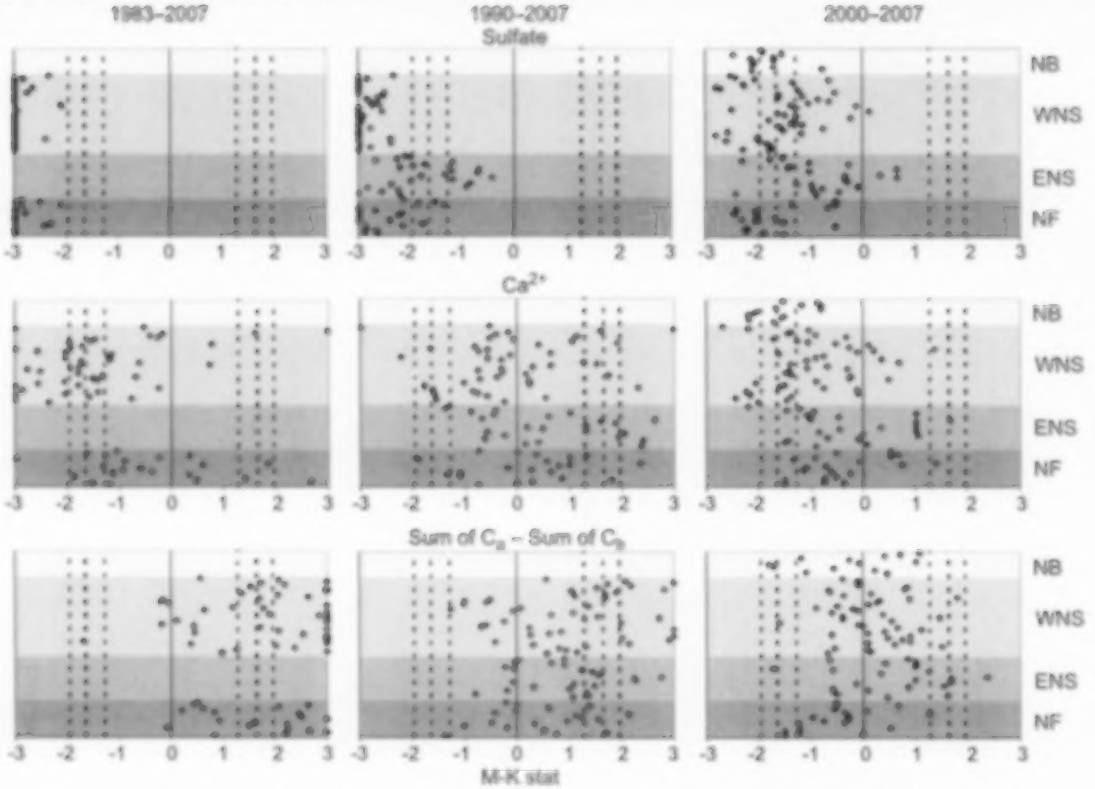


the major North American pollution sources. A general downward trend existed for SO_4^{2-} deposition throughout the period (Fig. 2), although the overall rate of decrease was moderated by an increase in deposition levels from about 1995 to 2000. We also note a temporary increase in deposition in the late 1990s.

Temporal trends of sea salt corrected SO_4^{2-} and H^+ ion wet deposition at the four CAPMoN sampling sites showed highly significant decreases from 1984 to 2007 (Table 1), in line with the SO_2 emission reductions that occurred in eastern North America during that period (Canada–United States Air Quality Agreement 2008). Both Kejimkujik and Bay d'Espoir showed significant decreases in NO_3^- wet deposition, while Jackson and Harcourt exhibited no significant trends.

In contrast, neither Kejimkujik nor Bay d'Espoir showed significant trends in Cl^- (Table 1) and Na^+ (not shown) wet deposition, while Jackson and Harcourt both showed significant increases in these sea salt related species. The Jackson site also showed significant increases in two other sea salt related species, K^+ and Mg^{2+}, while the other sites did not. Thus, SO_4^{2-} wet deposition decreased consistently at all sites, NO_3^- decreased at only Kejimkujik and Bay d'Espoir, and the sea salt related ions increased at Jackson and to some degree (i.e., only for Na^+ and Cl^-) at Harcourt. There were no statistically significant long-term changes in the precipitation

Fig. 4. Individual lake Mann–Kendall nonparametric trend statistic for SO_4^{2-} (top row), Ca^{2+} (middle row), and ANC_c (bottom row) for three sampling time windows: 1983–2007, 1990–2007, and 2000–2007. Significance of the M–K statistic is shown by vertical dotted lines, where ±1.6 is significant at >90%, ±1.9 is >95%, and ±2.1 is >99%.



amounts at the individual sites or over the region (Table 1), which means that changing precipitation levels did not contribute to the foregoing trends in ion deposition.

When assessing the 1990–2007 data window (Table 1), we still calculated significant decreasing trends in H^+ and SO_4^{2-} and some decreasing trends in NO_3^-. However, when using only data from the 2000–2007 window, we only note a decreasing H^+ value from Bay d'Espoir and a significant NO_3^- decrease at Jackson. From these results we suggest that SO_4^{2-} deposition has levelled out in this region since 2000 (as can be noted in Fig. 2).

Spatial lake chemistry trends

The west–east spatial lake trend chemistry reflected the generally westerly origins of anthropogenic SO_4^{2-} to this region (Fig. 3). Mean dissolved SO_4^{2-} concentrations for the arbitrarily chosen years 2000 to 2005 followed a west–east pattern of decreasing values, with the exception of a cluster of lakes centered in Kejimkujik National Park in WNS where values were lower than expected and in ENS where values were higher than the curve. We suspect that these values in WNS are caused by catchment soil SO_4^{2-} absorption due to the effect of wetlands in this region. Should these wetlands currently be SO_4^{2-} sinks, it suggests that recovery of their drainage waters will be delayed even further under lower deposition conditions, as they will most likely be releasing this ion for a longer period of time. The other possibility is that they may release large amounts of stored SO_4^{2-} in pulse events caused by periodic droughts, such as described by Dillon et al. (1997).

Another lake cluster in the ENS region between 62.5°W and 62.0°W had SO_4^{2-} concentrations slightly higher than expected from the regional curve. This group of lakes is located roughly 130 km east of the Halifax Regional Municipality, which has a population of approximately 400 000. The higher SO_4^{2-} levels in these lakes are probably due to industrial sources, transportation, and power generation in the Halifax area and support the work of Shaw (1986), who showed that this urban area affected the air quality of the surrounding region, especially to the east. Overall, these data suggest that there are no significant regional S sources affecting lake quality apart from the Halifax region.

Temporal lake chemistry trends

Water chemistry trends were calculated for each lake and plotted for the three time windows 1983–2007, 1990–2007, and 2000–2007. SO_4^{2-} shows a strong decreasing tendency in all regions over the three time windows (Fig. 4, top row), though it is clear that the trend weakens as the time windows become shorter and more recent. When using the whole time series, every WNS and NF lake shows a highly significant SO_4^{2-} decrease. The 1990–2007 series, which includes the

Table 2. Regional Mann–Kendall (M–K) statistics, *p* values (showing trend significances) at three time windows for major parameters.

	1983–2007		1990–2007		2000–2007	
NF (n = 14)	M–K	*p*	M–K	*p*	M–K	*p*
pH	–0.143	0.887	1.644	0.100	1.513	0.130
Gran ANC	1.099	0.272	0.553	0.580	2.067	0.039**
Ca^{2+}	–0.989	0.323	0.541	0.588	–0.783	0.434
Cl^-	0.105	0.917	2.566	0.010**	1.562	0.118
SO_4^{2-}	–4.268	<0.001***	–3.647	<0.001***	–2.618	0.009***
DOC	1.821	0.069*	0.902	0.367	1.973	0.049**
TN	0.097	0.922	–0.310	0.757	2.613	0.009***
$\sum C_b$	0.615	0.539	–0.677	0.498	–0.953	0.341
$\sum C_a$	–4.254	<0.001***	–3.610	<0.001***	–2.602	0.009***
$\sum C_b - \sum C_a$	2.800	0.005***	0.928	0.353	–0.666	0.506
WNS (n = 45)						
pH	0.378	0.706	0.534	0.593	0.632	0.527
Gran ANC	0.037	0.971	–0.062	0.950	2.367	0.018**
Ca^{2+}	–2.382	0.017**	–0.217	0.828	–1.585	0.113
Cl^-	0.027	0.978	1.126	0.260	–1.485	0.138
SO_4^{2-}	–4.292	<0.001***	–3.726	<0.001***	–1.971	0.049**
DOC	2.043	0.041**	2.551	0.011**	1.962	0.050**
TN	–0.850	0.395	–0.686	0.493	2.732	0.006***
$\sum C_b$	–0.911	0.362	–1.889	0.059*	–1.036	0.300
$\sum C_a$	–4.299	<0.001***	–3.732	<0.001***	–2.008	0.045**
$\sum C_b - \sum C_a$	3.237	0.001***	1.934	0.053*	0.198	0.843
ENS (n = 23)						
pH			2.689	0.007***	0.242	0.809
Gran ANC			1.130	0.258	2.210	0.027**
Ca^{2+}			1.028	0.304	–1.396	0.163
Cl^-			2.707	0.007***	0.667	0.505
SO_4^{2-}			–2.691	0.007***	–1.765	0.078*
DOC			0.587	0.557	2.195	0.028**
TN			–0.688	0.492	2.877	0.004***
$\sum C_b$			0.098	0.922	–0.259	0.795
$\sum C_a$			–2.685	0.007***	–1.795	0.073*
$\sum C_b - \sum C_a$			1.826	0.068*	0.706	0.480
NB (n = 13)						
pH					–0.797	0.425
Gran ANC					1.906	0.057*
Ca^{2+}					–1.762	0.078*
Cl^-					–2.557	0.011**
SO_4^{2-}					–2.010	0.044**
DOC					2.927	0.003***
TN					2.737	0.006***
$\sum C_b$					–1.237	0.216
$\sum C_a$					–2.035	0.042**
$\sum C_b - \sum C_a$					–0.245	0.806

Note: NF, Newfoundland; ENS, eastern Nova Scotia; WNS, western Nova Scotia; NB, New Brunswick; Gran ANC, Gran titration acid neutralization capacity; DOC, dissolved organic carbon; TN, total nitrogen; $\sum C_b$, sum of base cations; $\sum C_a$, sum of acid anions; $\sum C_b - \sum C_a$, acid neutralization capacity; *, trend is significant at 90%; **, significant at 95%; ***, significant at at >99%. The n value is the number of lakes in each subregion.

ENS lakes, shows that a strong decreasing pattern of lake concentrations is still evident in the three regions, while the 2000–2007 series, which included NB, shows a weaker SO_4^{2-} decrease.

The less emphatic pattern of SO_4^{2-} decrease in individual lakes is illustrated by the regional trend analysis (Table 2). The regional decrease in NF, WNS, and ENS is shown to be highly significant (>99%) using the 1983–2007 and 1990–2007 data windows (Table 2). When using the 2000–2007 data series, only NF still shows a regional decrease at the >99% confidence level; WNS and NB are now showing trends at >95%, while the ENS decrease is only significant at 92%. It is clear from this data that the wet deposition rate decrease discussed above is reflected in the shallower lake

Fig. 5. Individual lake Mann–Kendall (M–K) nonparametric trend statistic for Gran titration ANC (top row), dissolved organic carbon (DOC, middle row), and pH (bottom row) for three sampling time windows: 1983–2007, 1990–2007, and 2000–2007. Significance of the M–K statistic is shown by vertical dotted lines, where ±1.6 is significant at >90%, ±1.9 is >95%, and ±2.1 is >99%.

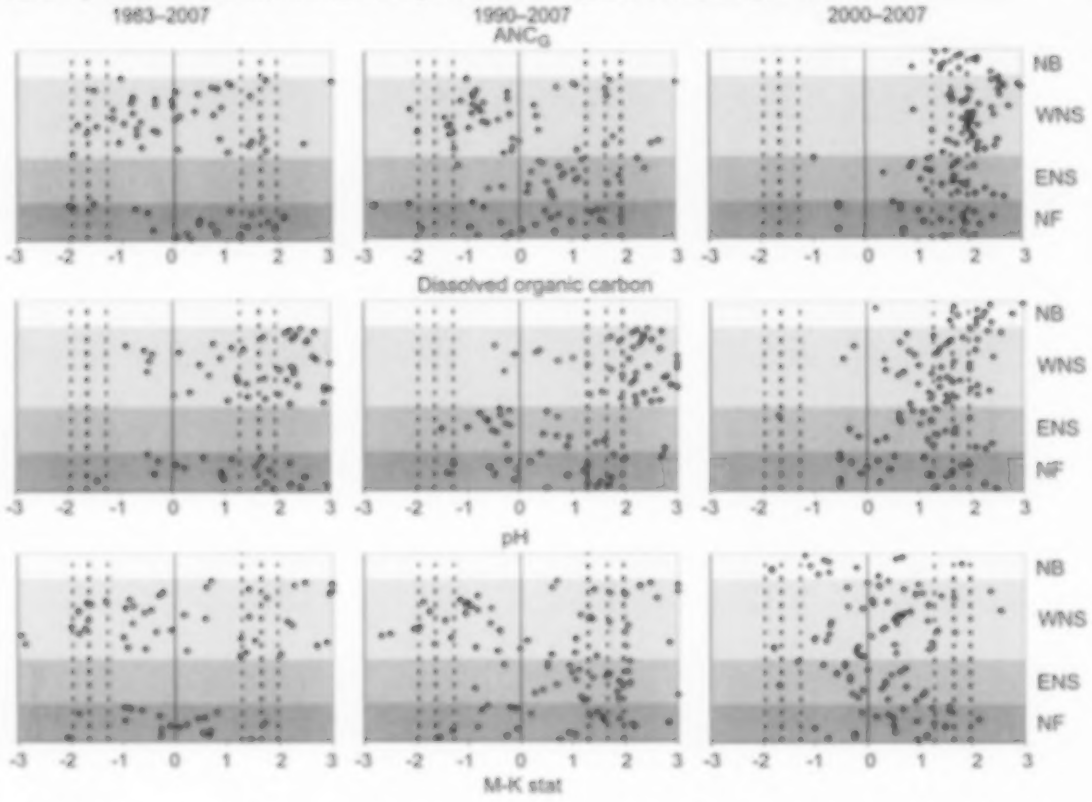


Fig. 6. Median subregional lake SO_4^{2-} trends from the lake monitoring network. The curves were smoothed using a spline interpolation approach.

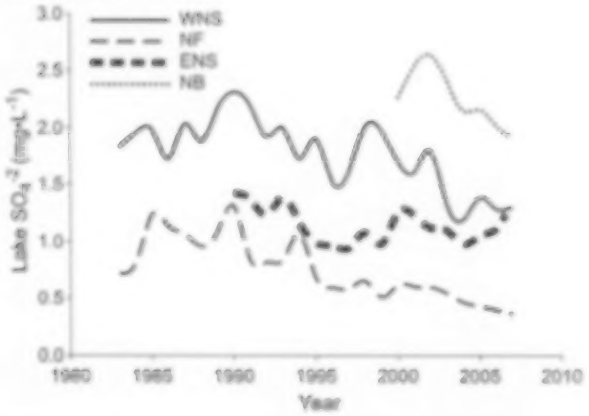
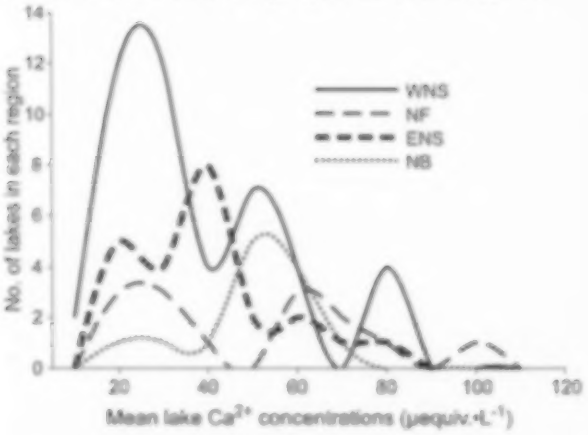


Fig. 7. Lake Ca^{2+} distribution in each of the of the study regions. The curves were smoothed using a spline interpolation approach.



SO_4^{2-} decrease. Unsurprisingly, sea salt corrected acid anions trends ($\sum C_a$) were identical to SO_4^{2-}, as Cl^- was not part of the equation, having been used to correct for sea salt. Of the other acid anions, NO_3^- was analyzed for all lake samples, but the very high prevalence of less than detectable values made trend analysis meaningless. Chloride concentrations were controlled by local marine storms and showed increases in NF and ENS from 1990 to 2000, but decreases in NB from 2000 to 2007. Though there was variability during the study period, there were no clear, long-term regional trends in this ion (Table 2).

Table 3. Long-term annual mean, minimum, and maximum temperature trends at climate stations located in or near sampling lake clusters.

Site		Slope	Intercept	r^2	p	Time range
Kejimkujik	Mean	0.0772	−147.1	0.353	0.002	1984–2007
(WNS)	Min.	0.1041	−206.2	0.493	<0.001	1984–2007
	Max.	0.0506	−88.8	0.159	0.036	1984–2007
Harvey	Mean	0.0743	−142.5	0.283	0.048	1984–2003
(NB)	Min.	0.1216	−241.8	0.467	0.004	1984–2003
	Max.	0.0273	−43.9	0.053	0.650	1984–2003
Malay Falls	Mean	0.1159	−225.2	0.602	0.001	1988–2006
(ENS)	Min.	0.1131	−224.9	0.509	0.002	1988–2006
	Max.	0.1195	−227.1	0.625	<0.001	1988–2006
Cheticamp	Mean	0.0739	−140.9	0.365	0.002	1984–2006
(ENS)	Min.	0.0736	−144.3	0.323	0.005	1984–2006
	Max.	0.0732	−135.3	0.364	0.002	1984–2006
RockyHarbour	Mean	0.1151	−225.4	0.461	0.002	1984–2007
(NF, west)	Min.	0.0934	−186.4	0.355	0.011	1984–2007
	Max.	0.1371	−265.0	0.520	0.001	1984–2007
TerraNova	Mean	0.1237	−241.7	0.516	0.002	1984–2007
(NF, east)	Min.	0.1233	−245.4	0.504	0.002	1984–2007
	Max.	0.1233	−236.2	0.510	0.001	1984–2007

Note: Slope and intercept calculated by regression analysis; r^2 and p values calculated using the Mann–Kendall approach. WNS, western Nova Scotia; NB, New Brunswick; ENS, eastern Nova Scotia; NF, Newfoundland.

Calcium is the most important base cation in these waters, after Na^+, which originates from sea spray. The only significant trend shown by Ca^{2+} in the whole study was a regional decrease in WNS using 1983–2007 data (Fig. 4, middle row; Table 2). As there were no trends in the 1990–2007 and 2000–2007, it suggests that the Ca^{2+} decrease only occurred at the beginning of the sampling period when SO_4^{2-} decreased and (or) because it was depleted from soils. Overall, in all other regions, the nonsignificant tendency for Ca^{2+} is negative.

ANC_c was effectively the difference between Ca^{2+} and SO_4^{2-}, as discussed above. ANC_c only showed a significant increase using WNS and NF 1983–2007 data (Fig. 4, bottom row; Table 2). As $\sum C_b$ showed no significant regional trends (>95%) at any time for any of the regions (Table 2), the ANC_c increase measured could only be caused by the SO_4^{2-} reduction.

Gran titration alkalinity (ANC_G) showed a surprising result (Fig. 5, top row). Under most conditions, we would expect ANC_G values and trends to be the same as those of ANC_c. However, whereas ANC_c increased significantly only at the beginning of the data series and only in WNS and NF, ANC_G showed significant regional increases ($p > 95\%$) in NF, WNS, and ENS and a slightly lesser increase ($p \sim 94\%$) in NB (Fig. 5, top row; Table 2) for the 2000–2007 period.

DOC increased everywhere in the 2000–2007 period (Fig. 5, middle row; Table 2), but at no other time. The trend analysis also shows significant increases in total nitrogen (TN) in all the regions using the 2000–2007 data. As N is incorporated into soil and soil pore waters organic matter, its increase is most likely related to the DOC increase. The end result of all the chemical changes that have occurred in the lakes is that the only significant increase in pH in the network occurred in ENS using the 1990–2007 period. Apart from this, there were no long-term changes in pH anywhere (Fig. 5, bottom row; Table 2).

Discussion

Our data show that the wet sulfur deposition reduction that occurred in this region was matched by decreases in regional lake SO_4^{2-} concentration (Fig. 6), as both media show highly significant reductions, especially in the earlier part of the data series. Visual comparison of annual S deposition and regional lake chemistry (Fig. 6) shows that year to year fluctuations are poorly matched, and we found it impossible to statistically correlate deposition and lake chemistry using simple, logical approaches. Nevertheless, we clearly show that long-term deposition SO_4^{2-} reductions are being followed in sampled lakes.

WNS results showed that 100% of lakes had strong SO_4^{2-} decreases when using 1983–2007 and 1990–2007 data series. NF, on the other hand, showed 100% of the sites with SO_4^{2-} decreases using the full data set and 90% with the 2000–2007 data. The trends in these regions therefore consistently showed that SO_4^{2-} concentrations in lakes decreased. In contrast, only 50% of ENS showed statistically significant reductions. The higher than expected SO_4^{2-} concentrations in ENS lakes suggest that lakes in the eastern part of Nova Scotia are also being affected by local sources.

With the measured decrease in H^+ deposition concurrent with the SO_4^{2-} decrease, we expected a widespread increase in the pH of lake waters, a result predicted by electroneutrality considerations and geochemical modeling (Clair et al. 2004). The only subregion that showed any regional pH increase was ENS and only for the 1990–2000 period. The unexpected lack of pH increase is probably due to increases in DOC, which will be further discussed below.

Sea salt corrected Ca^{2+} values in lakes of all four study subregions are very low compared with elsewhere in Canada (Fig. 7; Jeffries et al. 2005). As acid deposition increases in a region, catchment soils exchange incoming H^+ ions for bound base cations, the main cation usually being Ca^{2+}. The

cations are released into soil pore waters and eventually make their way into streams and lakes and are lost from the catchment. If the soils are formed from parent material high in base cations, such as limestone, then increasing acid rain not only increases base cation exports from catchments, but also increases HCO_3^- concentrations, which lead to higher alkalinity, a surprising and initially counterintuitive result (Kilham 1982).

If, on the other hand, soil C_b (Ca^{2+}, K^+, Mg^{2+}) concentrations are very low because of resistant or C_b-poor bedrock such as in our study sites, then increases in acid deposition will lead to initial increases in stream C_b concentrations as these are being flushed from soils, followed by decreasing values as the soils become depleted. Continued acid deposition on these soils may eventually lead to runoff water concentrations with much lower C_b values than before acidification, as the original source (soils) are now depleted. As the soil C_b reservoir in this region can only be replenished from bedrock with low C_b content, recovery of the soils and thus surface waters will need further acid deposition reductions and could take several decades to occur.

Clair et al. (2004) and Whitfield et al. (2006) used the Model of Acidification of Groundwater in Catchments (MAGIC) to predict that C_b concentrations in many NS stream waters would increase during high acid deposition periods and that values would then fall with reduced acid titration intensity and with lower amounts left in soils. Clair et al. (2004) also predicted that stream C_b concentrations would eventually reach values lower than before-acidification conditions and would remain lower at least until the 22nd century. Since we show only one significant decreasing Ca^{2+} trend in WNS and one other weakly significant trend in NB ($p = 0.08$), we suggest that sensitive areas of Atlantic Canada have now been depleted of most soil-exchangeable calcium and are in the last stage of the acidification process. This means that any increases in lake base cation concentrations can only come from weathering of the resistant bedrock under low acid deposition conditions.

Regional ANC_c trends only show significant increases when using the complete 1983–2007 data series in NF and WNS. The main reason for the ANC_c increase in the earliest part of the record is that acid anions were decreasing more rapidly than base cations during this period and not because of increasing base cations from renewed soil and geological weathering, which would suggest ecosystem recovery. The lack of significant ANC_c long-term trends suggests that since SO_4^{2-} concentrations have somewhat stabilized, there now needs to be an increase in C_b from natural weathering and (or) a further reduction in acid deposition to allow long-term increases in ANC_c associated with the recovery process.

The significant Gran titration alkalinity (ANC_G) increase in all regions from 2000 to 2007 was initially very surprising, as this parameter would be expected to behave similarly to ANC_c. However, as ANC_c is calculated using only base cations and acid anions, it does not take into account weak acids such as organic acids that are in solution. The Gran titration, on the other hand, does measure the effect of the weaker acids if they are present. As DOC molecules can contain substantial concentrations of natural organic acids (Perdue et al. 1980), the DOC increases measured from 2000 to 2007 are therefore the most likely reason for the ANC_G increases.

Most DOC in headwaters such as our monitoring sites is a by-product of the decomposition of plant matter in catchment soils. The chemical composition of DOC includes organic anion site concentrations (Oliver et al. 1983), which, because of their acid dissociation constant ranges (pK_a), can either provide H^+ ions (acidifying) or complex them (buffering) in fresh waters (these types of acids are called amphoteric acids) depending on ambient pH (Clair et al. 1992). The end result of this complex chemistry is that at high DOC concentrations, organic anions increase the acidity of waters with relatively higher pH values (>5.5), but can nevertheless act as buffers in more acidic conditions.

As DOC concentrations across the three study regions were relatively high, ranging between 4 and 9 $mg \cdot L^{-1}$, this ensured that carboxylic acid functional groups played an important role in the acid–base chemistry of these waters (Clair et al. 1992). The increase in DOC, causing an increase of organic acid exchange sites, is therefore probably the main reason for the lack of pH increases in our regions, though the interaction between organic acids and the rest of the lake water solution is difficult to assess, and it would require complex analyses such as those done by Erlandsson et al. (2010) to better quantify cause–effect relationships.

Why DOC is increasing in the latter part of the record is a difficult question to answer, though this phenomenon has also been observed in much of North America and Europe (Evans et al. 2006; Worrall et al. 2004). There are two main explanations currently being promoted in the literature to explain regional DOC increases that are being measured. The first one (Evans et al. 2006) is that DOC increases are due to the effect of SO_4^{2-} decreases in soils. They suggest that as sulfate is reduced in soil solution, organic anion concentrations and thus DOC increase to maintain electroneutrality. The converse to this idea is that under higher soil SO_4^{2-} concentrations, DOC solubility is suppressed. Another possible theory explaining regional increases of DOC is that they are caused by increasing precipitation and temperature, which enhance soil organic matter decomposition and transportation to streams and lakes.

Neff and Asner (2001) reviewed a number of first-principle soil DOC generation models and identified hydrology (and thus precipitation) and temperature as the main drivers of DOC production and transport in soil waters. The CAP-MoN sites used in this study have not shown significant tendencies in precipitation, so that changes in that variable cannot be used to explain the DOC change. However, analysis of regional temperature trends are much more suggestive. We calculated trends in mean annual temperature, as well as mean annual minimum and maximum values at meteorological sites containing at least 20 years of data located in or near lake clusters and found a clear, unambiguous increase in temperatures at all sites (Table 3). Mean annual increases over the sampling period ranging from 1.5 to 2.5 °C, depending on the region and its proximity to the ocean.

Our data therefore tend to support the climatic theory for explaining the DOC increase. Our measured subregional DOC increases are similar in all sampling regions, while SO_4^{2-} concentrations and reductions are much greater in the western part of Atlantic Canada than in the east. Under the hypothesis of Evans et al. (2006), we would therefore expect the increase in DOC concentrations to be greater in WNS

than in NF, which is not the case (Fig. 5, middle row, right panel). Moreover, the regional DOC increase also coincided with a flattening in the SO_4^{2-} wet deposition reduction curve.

The DOC increases are somewhat surprising, as Clair et al. (2008) found decreasing DOC concentration trends and no export trends from two streams located in the Kejimkujik National Park region, though they used data that extended from 1983 to 2004. The difference between studies may not necessarily be contradictory, as it is clear that the increase that we measured occurred between 2000 and 2007, so that a few years' additional data could have caused the significant shift measured.

Our view is supported by Worrall et al. (2004), who thoroughly discussed all possible explanations for increases in DOC in rivers from the United Kingdom and who suggested that increases in temperature, potentially tied in with land use changes, were the most likely cause of the changes they measured. As our sampling lakes were generally found in undisturbed areas, the land use possibility did not apply to our study. Our results therefore suggest that the hypothesis that temperature drives the DOC increase is the most likely mechanism in our region. The debate concerning the causes of the Northern Hemispheric DOC increases will most likely only be settled with meta-analyses of data from large numbers of studies. As Erlandsson et al. (2010) state, it is quite possible that more than one factor is involved in controlling DOC leaching from catchment soils, considering the large range of soil, deposition, and climatic variations in the Northern Hemisphere.

Our results show the importance of the sampling time window in accurately determining whether acid wet deposition changes have been reflected by changes in lake chemistry. The 25-, 18-, and 8-year records from NF and WNS were compared with the shorter ones from the other sampling subregions and confirmed the consistent decreasing trend in SO_4^{2-} as well as the lack of C_b or pH increases that would indicate recovery from acidification. Comparison of time window trends also showed a regional increase in DOC, TN, and ANC_G, which were measured everywhere using only 2000 to 2007 data.

The results from our inorganic ion trends were also compared with those from Skjelkvåle et al. (2005), who reported that Atlantic Canada (with nearby northern Maine, USA) was the only region of 11 in western Europe and North America that still had decreasing pH and ANC_c values. We show that base cations and pH concentrations in sensitive Atlantic Canada lakes seem to have bottomed out, but have not changed direction to indicate a recovery. The increase in DOC measured since 2000 probably contributes to lack of recovery in pH, though the C_b increase necessary to cause a sustained ecosystem recovery is not expected to occur for a long time because of its exhaustion from soils and the slow weathering rates occurring in this region's bedrock.

Our results show that the legacy of a problem that began in the 1940s and peaked in the early 1980s is still with us and will continue causing problems in Atlantic Canada for several decades to come. Water chemistry conditions suitable to allow the survival and thriving of Atlantic salmon, the most visible symbol of the acidification problem in much of Nova Scotia, have not improved in the past 30 years. Geochemical modeling and theory suggest that they can only recover under lower acid deposition levels than are currently being endured and after several decades of natural weathering to allow base cation replenishment of soils from resistant bedrock.

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Climate change modulates structural and functional lake ecosystem responses to introduced anadromous salmon

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Abstract: We integrated limnological, paleolimnological, and fisheries analyses in Tuya Lake, British Columbia, Canada, to explore the effects and interactions of climate warming and sockeye salmon introductions on northern lake ecology. We tracked millennially unprecedented, climate-correlated changes in inferred lake production, stratification, and trophic structure since the mid-1800s, most likely resulting from declining ice cover and enhanced stratification. Post-1970s algal (diatom) species turnover, coeval across several remote northern Cordilleran lakes, marked an apparent increase in warming and the induction of inferred nitrogen deficiencies in Tuya Lake. Lower post-stocking phosphorus (P) and nitrogen (N) concentrations and a strong P-modeled salmon biomass correlation ($r^2 = 0.87$) indicated salmon production reduced epilimnetic nutrient availability. Post-stocking chlorophyll reductions, late-summer algal dominance by heterocystous cyanobacteria and low-N-tolerant diatoms, and a strong chlorophyll-modeled salmon biomass correlation ($r^2 = 0.87$) indicated that salmon influenced lake productivity, most likely by enhancing climate-induced N-deficiencies. Predicted smolt-biomass nutrient exports were minimal, with post-introduction nutrient reductions likely related to planktivory and enhanced sedimentation losses. Our study highlights how climate warming changes northern lake ecosystem structure and functioning, influencing responses to subsequent stresses.

Résumé : Nous intégrons des analyses limnologiques, paléolimnologiques et halieutiques dans le lac Tuya, Colombie-Britannique, Canada, afin d'explorer les effets et les interactions du réchauffement climatique et des empoissonnements de saumons rouges sur l'écologie d'un lac boréal. Nous avons recherché les changements sans précédent à l'échelle du millénaire reliés au climat dans les données déduites de production, de stratification et de structure trophique depuis le milieu des années 1800, résultant le plus vraisemblablement du déclin de la couverture de glace et de l'augmentation de la stratification. Après les années 1970, le remplacement des espèces d'algues (diatomées), phénomène simultané dans plusieurs lacs éloignés de la cordillère, marque une augmentation apparente du réchauffement et l'apparition de carences présumées en azote dans le lac Tuya. Des concentrations réduites de phosphore (P) et d'azote (N) après l'empoissonnement et une forte corrélation ($r^2 = 0,87$) modélisée entre P et la biomasse des saumons indiquent que la production des saumons réduit la disponibilité des nutriments dans l'épilimnion. Les réductions de la chlorophylle après l'empoissonnement, la dominance des cyanobactéries hétérocystes chez les algues en fin d'été, la présence de diatomées tolérantes aux faibles concentrations de N et une forte corrélation ($r^2 = 0,87$) entre la chlorophylle et la biomasse modélisée des saumons montrent que les saumons affectent la productivité du lac, le plus vraisemblablement en accentuant les carences en N provoquées par le climat. Les exportations prédites de nutriments en forme de biomasse de saumoneaux sont minimales, car les réductions de nutriments après l'empoissonnement sont vraisemblablement liées à la planctonophagie et aux pertes accrues vers les sédiments. Notre étude met en lumière comment les changements dus au réchauffement climatique dans la structure et le fonctionnement d'un lac boréal influencent les réactions aux stress subséquents.

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Introduction

Climate is a principal driver of global aquatic ecosystems. Climate variability modulates the physiologies, phenologies, and distributions of species, community compositions and interactions, and ultimately shapes the structure and function of ecosystems (Walther et al. 2002). While recent warming has broadly impacted global ecosystems (Parmesan and Yohe 2003), regional-scale climatic and ecological responses have been highly variable (Walther et al. 2002; Smol et al. 2005). Such ecological complexity may arise from the intrinsic spatial and temporal dynamics underlying both ecological and climate systems (Walther et al. 2002; Burkett et al. 2005). Compounding ecological stresses, however, may interact with climate change, accounting for additional, often unexpected ecological variability (Christensen et al. 2006; Schindler and Smol 2006; Smol 2010). Predicting aquatic ecosystem responses to multiple stressors is complicated by the unique timescales and intensities upon which differing ecosystem drivers operate. In particular, the influences and interactions of long-term forcing mechanisms, such as climate change, may appear cryptic from contemporary ecological perspectives (e.g., Hughes and Connell 1999). Climate warming has occurred for at least the past two centuries (IPCC 2007), undoubtedly modifying the structural and functional development of modern aquatic ecosystems, and thus acting to precondition ecosystems to subsequent stressors (i.e., ecosystem "climate conditioning"). As stresses on global freshwater rise, recognizing such past ecosystem changes will likely be essential in predicting ecological complexities arising from compounding stressors.

High-latitude aquatic ecosystems are disproportionately sensitive to climate change, as evidenced by recent warming-induced state changes in northern aquatic communities (Smol et al. 2005; Prowse et al. 2006). Climate change influences northern and alpine lake ecology, principally through variations in temperature and precipitation (Hauer et al. 1997; Rouse et al. 1997). Temperature regulates the thermal and optical parameters important to lake production, such as the extent and timing of ice cover (Schindler 1997; Magnuson et al. 2000; Cahill et al. 2005) and stratification and mixing patterns (De Stasio et al. 1996; Cahill et al. 2005). Temperature and precipitation also indirectly influence lake chemistry and food web dynamics through metabolic controls on biological production (Karlsson et al. 2005), modifications to lake and catchment nutrient cycling, and changes in the extent and timing of hydrological delivery (Hauer et al. 1997; Rouse et al. 1997). Precipitation and temperature also affect dissolved organic carbon (DOC) in lakes, which can influence algal production by modifying photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) penetration (Pienitz and Vincent 2000; Leavitt et al. 2003).

Despite their remote locations, northern lakes are increasingly influenced by a range of local environmental stressors (McCarthy et al. 2004; Schindler and Smol 2006). The intentional introduction of non-native fish, a common approach to enhance, restore, and create fisheries (Cowx and Gerdeaux 2004), has resulted in complex freshwater ecosystem responses (Eby et al. 2006). In some lakes, introduced fish have stimulated nutrient availability and primary production via enhanced nutrient cycling and novel coupling of benthic and pelagic energy flows (Leavitt et al. 1994; Schindler et al. 2001). Introduced planktivores, however, also elicit strong size selection on zooplankton, altering population abundances and community structure (Brooks and Dodson 1965; Kyle 1996). Enhanced planktivory elicits varied responses at lower trophic levels, ranging from cascading enhancement of algal standing crops (Carpenter and Kitchell 1993; Vanni and Layne 1997) to reduced algal production via enhanced nutrient sedimentation (Houser et al. 2000).

Lake ecosystem responses to fish introductions are further complicated when species with diverse life histories, such as anadromous and semelparous Pacific sockeye salmon (*Oncorhynchus nerka*) are stocked, owing to simultaneous "bottom up" (e.g., nutrient controls) and "top down" (e.g., planktivory) influences on lake food webs (Schindler et al. 2003). Pacific salmon also mediate bi-directional nutrient flows (e.g., carcass influxes vs. juvenile biomass-sequestered effluxes) in freshwater nursery ecosystems (Moore and Schindler 2004; Scheuerell et al. 2005), which is a predicted net nutrient export mechanism in "barren lakes" where salmon are stocked to supplement terminal fisheries, but returning spawner passage is impeded (Moore and Schindler 2004). Few lake data exist to evaluate the ecological implications of such nutrient exports, particularly in relation to planktivory effects on food web structure and productivity. Moreover, despite the prevalence of non-native fish stocking, and the pervasive effects of climate change, the cumulative impacts and interactions of these stressors on lake ecosystems remain poorly understood.

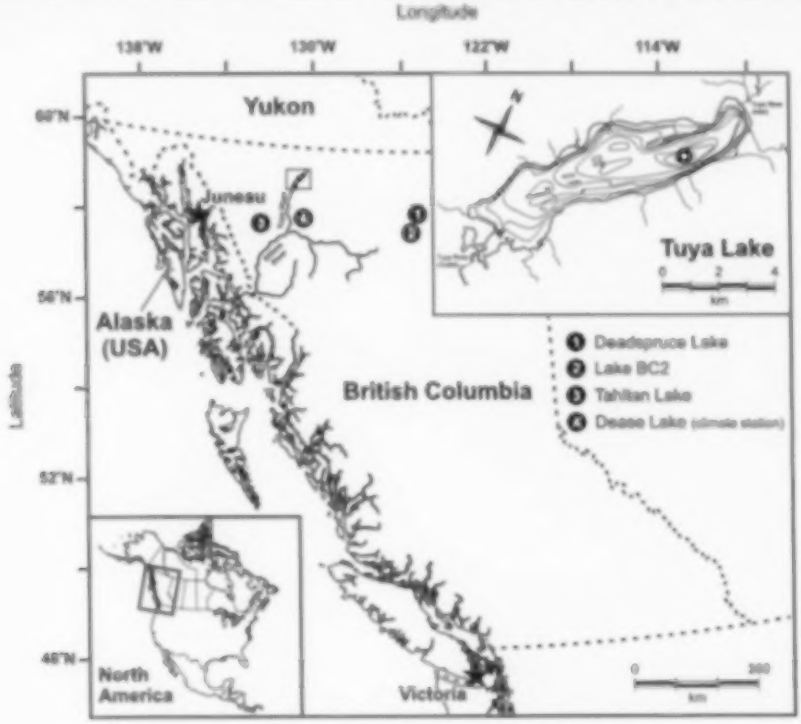
We used limnological, fisheries, and paleolimnological methods in a northern Canadian Cordilleran lake to explore our hypothesis that climate warming has influenced lake ecosystems (i.e., "climate conditioning") in ways that modulate the effects of subsequent stressors (i.e., non-native salmon stocking). Our study established unprecedented warming-induced changes in lake physics, nutrient cycling, and lake productivity that preceded the recent salmon introductions, and most likely modulated the impacts of this stocking on lake productivity. Our results highlight the complexity in ecosystem responses to stressors varying on different timescales, and the importance of understanding the long-term "climate conditioning" of northern lake ecosystems, as previous warming influences may shape ecosystem responses to subsequent stresses.

Materials and methods

Study area

Our study focused on remote, subalpine Tuya Lake (59°05′N, 130°35′W, 1117 m a.s.l.), located in the northern Cordillera of British Columbia, Canada (Fig. 1). The region has experienced marked warming (1.7 °C) over the instrumental record (52 years), at approximately three times the global centennial average (BCMWLAP 2002). At present, regional climate variability is modulated by the Pacific Decadal Oscillation (PDO; Stahl et al. 2006), characterized by interdecadal (20–30 years) warm (ca. 1925–1947, 1977–1998) and cold (ca. 1890–1925, 1947–1977) regimes (Mantua et al. 1997). Significant regional warming has occurred in spring (+ 3.8 °C), advancing snow melt by 9 days·decade^{-1}, and ice-off dates by 3 days·decade^{-1} over the period 1945–1993 (BCMWLAP

Fig. 1. Location of Tuya Lake, British Columbia, in the northern Canadian Cordillera with the sites (1) Deadspruce Lake, (2) BC2 Lake, and (3) Tahltan Lake mentioned in the text. The inlaid bathymetric map (6 m contours shown) indicates the location of core retrieval (open circle).



2002). Ice currently persists from November until mid-June, with the lake typically thermally stratified through September (Mathias 2000).

Tuya Lake is deep and currently oligo-mesotrophic (Table 1). The watershed is underlain by granitic bedrock, overlain with thick glacial till, and spans the Spruce–Willow–Birch and Alpine Tundra biogeoclimatic zones, characterized by sparse arboreal vegetation (mainly *Picea*, *Salix*, *Betula* spp.) and extensive tundra grasslands (Coombes 1986). Tuya Lake drains to the Pacific Ocean, but is believed to be naturally devoid of anadromous fish, owing to downstream waterfall and velocity barriers (PSC 1988; Mathias 2000). Since 1991, however, hatchery-raised juvenile sockeye salmon, originating from nearby Tahltan Lake, British Columbia (Fig. 1), have been stocked in Tuya Lake (Mathias 2000) at varying intensities (0–4.7 million fish·year^{-1}). Juveniles mature for 1–3 years before outmigration, but some sockeye salmon appear to have residualized (i.e., kokanee), and remain within the lake over their life history (Beere 2002). Sexually mature adults cannot return to the lake and are harvested in international gillnet and terminal fisheries.

Limnological and paleolimnological data

Limnological monitoring data were used to quantify lake conditions prior to and during the salmon introductions. Archival late-summer (September) nutrient (total phosphorus, dissolved inorganic nitrogen), and algal (chlorophyll *a*) measurements were provided by Fisheries and Oceans Canada (DFO) and the British Columbia Ministry of the Environment (Table 1). Additional chemical (nutrients, chlorophyll *a*, pH, temperature, oxygen) and biological (phytoplankton and zooplankton) samples were taken in September 2003 (Table 1).

Paleolimnological analyses were conducted to establish the natural range of ecosystem variability and multitrophic lake responses to both climate warming and fish introductions. All analyses were conducted on a 45 cm long gravity sediment core retrieved from the depositional zone of Tuya Lake (52 m depth), and sectioned at 1 cm intervals using a vertical extruder (Glew et al. 2001). The core geochronology was established using radioisotopic (^{210}Pb, ^{14}C) dating techniques. ^{210}Pb and ^{214}Bi activities were recorded by low-background gamma spectrometry (Appleby 2001) on freeze-dried, homogenized, bulk sediment samples over the top 16 cm of the core. ^{210}Pb ages were determined using the constant rate of supply (CRS) model (Binford 1990). A basal accelerator mass spectrometry (AMS) ^{14}C date was attained from a conifer needle at 44–45 cm. This analysis was conducted at the Lawrence Livermore Center for Accelerator Mass Spectrometry, and the date calibrated using Calib 5.0.2 (Reimer et al. 2004).

Climate and paleoclimate data

The influences of interannual climate variability on Tuya Lake were assessed by comparing our limnological time series with annual and late-summer temperature (mean, maximum, and minimum) and precipitation (rain, snow, total precipitation) data from the closest meteorological station (Dease Lake, British Columbia; 58°26′00″N, 130°01′27″W;

Table 1. Modern physicochemical and biological parameters of Tuya Lake, British Columbia, Canada.

Parameter		Pre- or post-introduction of sockeye salmon
Surface area (km^2)[a]	29.5	
Watershed area (km^2)[a]	466.16	
Mean/max. depth (m)[a,b]	23/54	
Volume ($\times 10^6 \cdot m^{-3}$)[b]	7.08	
Late-summer total phosphorus ($\mu g \cdot L^{-1}$)	14.0	Pre-salmon (1986)[c]
	8.4–11.8	Post-salmon (1992–2003)[c,d]
Late-summer dissolved inorganic nitrogen ($\mu g \cdot L^{-1}$)	230.0	Pre-salmon (1986)[c]
	92.1, 180.0	Post-salmon (1991, 2003)[c,d]
Late-summer total nitrogen ($\mu g \cdot L^{-1}$)	249.0	Post-salmon (2003)[e]
Annual epilimnetic chl *a* range ($\mu g \cdot L^{-1}$)	2.0–3.0	Pre-salmon (1990)[f]
Late-summer epilimnetic chl *a* ($\mu g \cdot L^{-1}$)	1.0–1.6	Post-salmon (1994–2003)[c,d]
Seston POC:PON (molar)	9.8	Post-salmon (2003)[e]
Mean epilimnetic/hypolimnetic pH	7.8/7.2	Post-salmon (2003)[e]
Dissolved organic carbon ($mg \cdot L^{-1}$)	4.3	Post-salmon (2003)[e]
Mean late-summer Secchi depth (m)	5.0	Pre-salmon (1986–1990)[f]
	6.0	Post-salmon (1991–1995)[f]
Dominant zooplankton groups[b]	*Bosmina*, *Daphnia*, *Cyclops*, rotifers, *Skistodiaptomus*, *Holopedium*, calanoid copepods, *Diaphanosoma*, harpacticoid copepods	
Resident fish species[f]	Arctic grayling (*Thymalus arcticus*), bull trout (*Salvelinus confluentus*), long nose sucker (*Catostomus catostomus*), burbot (*Lota lota*), prickly sculpin (*Cottus asper*), slimy sculpin (*Cottus cognatus*)	
Introduced fish species	Sockeye salmon (*Oncorhynchus nerka*) (1991)	

Note: Chl *a*, chlorophyll *a*; POC, particulate organic carbon; PON, particulate organic nitrogen.
[a]This study.
[b]Mathias (2000).
[c]Coombes (1986).
[d]K.D. Hyatt, unpublished data.
[e]PSC (1994).
[f]Beere (2002).

Fig. 1). All climate data were acquired from the Environment Canada National Climate Archive (climate.weatheroffice.ec.gc.ca). Long-term climate-lake interactions were explored by comparing our proxy data with published regional (Szeicz and MacDonald 1995; Davi et al. 2003; Luckman and Wilson 2005) and pan-Arctic (Overpeck et al. 1997) temperature reconstructions.

Past anadromous fish production in Tuya Lake

Sedimentary stable nitrogen isotopes ($\delta^{15}N$) were analyzed to assess potential prehistorical anadromous salmon utilization of Tuya Lake. Sedimentary $\delta^{15}N$ signatures can reflect salmon-derived nutrient influxes in many nursery ecosystems (Gregory-Eaves et al. 2009; Selbie et al. 2009), and have been reliably used to infer past salmon population dynamics (e.g., Finney et al. 2002; Schindler et al. 2005; Selbie et al. 2007). Sedimentary organic matter $\delta^{15}N$ was analyzed following standard methods (Talbot 2001) on a Finnigan Delta Plus mass spectrometer, with analytical uncertainty $\pm$ 0.2‰. Isotope values are expressed in delta notation (δ = [[R sample-(R standard)$^{-1}$]–1]·1000, R = $^{15}N \cdot {}^{14}N^{-1}$) relative to atmospheric N_2, the international standard. The Tuya Lake $\delta^{15}N$ time series was compared with $\delta^{15}N$ records from sockeye salmon lakes in Alaska (Finney et al. 2002; Schindler et al. 2005) and the Pacific Northwest (Selbie et al. 2007) that receive a range of spawner densities, and to the mean $\delta^{15}N$ values of surface sediments from 100 lakes in British Columbia and Alaska where sockeye salmon had not been introduced (nonsalmon lakes) (Selbie et al. 2009).

Subfossil diatom and cladoceran assemblages

Sedimentary diatom and cladoceran subfossils were analyzed to infer past variability in lake trophic status and changes in algal and invertebrate communities. Diatom samples were prepared for light microscopy following methods similar to Battarbee et al. (2001). Siliceous valves were isolated from homogenized wet sediments (~0.5 g) by treatment with 10% HCl (carbonates) and 30% H_2O_2 (organics). Dilutions were air-dried on cover slips and mounted on slides using Naphrax® medium (refractive index = 1.74). A minimum of 300 diatom valves per interval were enumerated and identified along central parallel transects at 1000× magnification. Taxonomic identification followed that of Krammer and Lange-Bertalot (1986–1991) and Cumming et al. (1995). The diatom *Aulacoseira subarctica* displayed pronounced morphological variability in Tuya Lake, and a cell size time series was recorded and presented as the population percentage exhibiting a distinct narrow valve diameter (<5 μm). To relate changes in the life history strategy of *A. subarctica* to climate warming and salmon introductions, full population size distributions (valve diameter, mantle height; n = 500

per sample) were compared prior to warming, following warming, and after the salmon introductions.

Subfossil cladoceran samples were prepared following the procedures of Korhola and Rautio (2001). Chitinous remains were separated from wet sediments (~5 g) by heated deflocculation in 10% KOH, and rinsing through a 37 μm sieve. The retained fraction was volumetrically standardized (10 mL) and stained with a safranin–glycerin solution. Aliquots of 50 μL were mounted on slides, and a minimum of 50 individuals identified and enumerated at 400× magnification in each interval. For each taxon, the most abundant remain was used to calculate individuals per sample, and total cladoceran densities were expressed as flux estimates. Cladoceran taxonomy followed Sweetman and Smol (2006) and taxonomic references therein. Where species-level determinations were not possible, taxa were grouped to the lowest distinguishable level (e.g., *Alona guttata/barbulata*, *Bosmina* spp., *Daphnia pulex* group).

Lake paleoproduction and organic matter sedimentation and provenance

Past lake primary production and organic matter sources and deposition were assessed using multiple independent proxies. Sediment organic and carbonate contents were estimated using standard loss-on-ignition (LOI) analyses (Dean 1974). Samples were dried at 105 °C, then combusted at 550 °C for 2 h (organics) and further at 950 °C for 2 h (carbonates). Weight differences relative to dry sediments were used to determine sediment constituents, and carbonate estimates were corrected for non-evolved fractions (e.g., oxide). Bulk sedimentary nitrogen ($\%N_{sed}$) and carbon content ($\%C_{sed}$) were analyzed on freeze-dried, homogenized, bulk sediments (Meyers and Teranes 2001). The $\%N_{sed}$ and $\%C_{sed}$ were measured on a Carlo Erba elemental analyzer with analytical precision better than ±5% of the sample value. Sediment ratios of carbon to nitrogen (C:N) were used to assess terrestrial (C:N > 20) versus aquatic (C:N < 10) organic source material (Meyers and Teranes 2001; Selbie et al. 2009). Sedimentary biogenic silica ($BSiO_2$), an estimate of siliceous algal production (diatoms and chrysophytes), was attained by standard wet alkaline (Na_2CO_3) extraction on freeze-dried, homogenized sediment samples (~20 mg), and analyzed at time steps against calibrated Si standards by absorbance spectrophotometry (LKB Ultrospec II; Conley and Schelske 2001). Absorbency readings were converted to $BSiO_2$ fluxes relative to sediment density and time.

Sockeye biomass and nutrient flux modeling

A mass balance model was constructed to estimate biomass-mediated nutrient (N and P) fluxes resulting from salmon introductions to Tuya Lake. Salmon biomass inputs principally occur through stocked fry mortality because adults cannot naturally return to spawn (barrier falls), while exports result from smolt emigration to the Pacific Ocean. Fry biomass inputs were calculated annually using the 1991–2003 mean fry mass (0.13 g). As part of an upstream migration study in 2002, 119 adult sockeye were released above the barrier falls, and this biomass (2.72 kg·fish^{-1}) was included in the 2002 input estimate. Annual smolt biomass values were calculated relative to population proportions of freshwater residence (e.g., 1, 2, 3 years). Population age structure was determined by examining otoliths and scales from adults harvested in the terminal fishery (juveniles are thermally banded prior to release). Population proportions of freshwater residence were then back-calculated and total biomass exports estimated using average smolt weights recorded from 1993–1999 (1 year = 9.5 g, 2 years = 26.8 g, 3 years = 37.3 g; Mathias 2000; P. Etherton, unpublished data). As data on fry mortality and smolt outmigration for Tuya Lake are sparse, continuous estimates for these parameters were extrapolated from nearby Tahltan Lake, B.C., the brood-stock source. As Tuya Lake is more productive, with lower piscivory and larger smolts (Mathias 2000), conservative adjustments reflecting differences in yearly fry mortality (–20%) and smolt out-migrant numbers (+20%) were made, which generally agreed with the estimates obtained from available Tuya Lake field data (Mathias 2000). The sensitivity of predicted nutrient export and lake nutrient concentration parameters to higher smolt outmigrations was explored by increasing smolt out-migrants in the model to match fall fry densities captured in available hydroacoustic surveys (e.g., +40%, K.D. Hyatt, unpublished data).

Nitrogen and phosphorus fluxes were estimated using mean smolt (P_{smolt} = 0.43%; N_{smolt} = 2.49%) and adult (P_{adult} = 0.38%; N_{adult} = 3.04%) wet tissue values from the literature (see Moore and Schindler 2004). As mean sockeye fry N and P contents were not available in the literature, they were measured on whole, homogenized, hatchery-raised fry to be stocked in Tuya Lake. Fry P content (n = 8) was analyzed by ICP atomic emission spectrometry with a Varian Vista Pro AX CCD analyzer (analytical precision ± 8.7% of the sample value) on ground, ashed, and acid-digested (HNO_3 and HCl) tissues. Fry N content (n = 10) was analyzed on a Carlo Erba elemental analyzer (analytical precision better than ± 5% of the sample value). Mean wet weight sockeye fry P and N contents were P_{fry} = 0.20% and N_{fry} = 1.60%. Annual salmon-mediated nutrient transfers (net export in all years) were derived from import and export differences.

The influences of salmon biomass-mediated nutrient fluxes on N and P availability in Tuya Lake were determined by estimating lake nutrient changes relative to modeled smolt N and P exports and lake euphotic volume. Effects of salmon rearing on lake nutrients (total phosphorus, TP) and primary production (chlorophyll *a*, chl *a*) were explored via comparisons of modeled salmon biomass estimates with available limnological data. Continuous TP and chl *a* time series were developed for comparison with pre-stocking conditions. These values were generated from the strong empirical relationships between measured TP and chl *a* and modeled smolt biomass.

Numerical analyses

Detrended correspondence analysis (DCA; Hill and Gauch 1980) was used to determine the timing and magnitude of compositional changes in the sedimentary diatom and cladoceran assemblages over the past millennium using CANOCO version 4.5 (ter Braak and Šmilauer 2002). DCA analyses were conducted on untransformed species data. Rare taxa were down-weighted to account for analytical sensitivity, and detrending was by segments (Hill and Gauch 1980). Time series of species turnover are presented as DCA axis 1 sample scores (standard deviation units).

Relationships between lake data series and instrumental and paleoclimate data were explored using Pearson correlations with Bonferroni-adjusted probabilities. Time series analyses on the paleoenvironmental data were performed on both the raw data and those for which minor first order temporal autocorrelation had been sequentially removed by logarithmic and first-difference transformations (see Verleyen et al. 2004). Comparison of these analyses demonstrated that the paleoclimatic–paleolimnological relationships were driven by long-term trends consistent with directional climate warming, which are removed by first-differencing procedures. Given the time-integrated nature of lake sediment records (e.g., multi-annually smoothed) and the long-term directional development of climate warming, only the analyses of raw time series were included in our study, consistent with our objectives and previous approaches (see Bunting et al. 2007) to quantitatively assess long-term climatically mediated ecosystem changes.

Results

Sediment chronostratigraphy

Sedimentary ^{210}Pb activity exhibited a characteristic exponential decay with depth, with the total unsupported ^{210}Pb inventory contained in the top 12 cm of the core (Fig. 2). A strong relationship between log ^{210}Pb activity and cumulative dry mass ($r^2 = 0.91$) indicated negligible sediment mixing (Fig. 2). The basal calibrated AMS ^{14}C date (CAMS No.12446) revealed a maximum age for the core of 1016 AD (±135 years; 2σ error). An age model was constructed by fitting a 2nd order polynomial curve through the core top (2003) and all radioisotopic (^{210}Pb, ^{14}C) dates ($r^2 = 0.99$), which was generally consistent with a simple extrapolation model based upon cumulative dry mass assuming constant sedimentation (Fig. 2; Binford 1990).

Past anadromous fish use of Tuya Lake

The sedimentary δ^{15}N time series from Tuya Lake was characterized by generally low isotopic values and complacent trends in contrast to those observed in naturally producing sockeye salmon nursery lakes (Fig. 3). In general, δ^{15}N signatures were most similar to those from British Columbia and Alaska nonsalmon lakes, supporting the assertion (e.g., PSC 1988) that Tuya Lake was a system devoid of Pacific salmon production prior to sockeye salmon stocking in 1991.

Lake paleoproduction and organic matter deposition

Consistent trends were observed in our independent indicators of past lake production and associated organic matter (OM) sedimentation (Fig. 4). Biogenic silica ($BSiO_2$) fluxes (siliceous algal production) were strongly correlated to regional and pan-Arctic temperatures (Table 2), exhibiting low and stable values throughout the early record followed by increases coeval with the regional culmination of the Little Ice Age (Hu et al. 2001) and the warming after the mid-1800s (Table 2; Fig. 4*d*). The lack of diatom valve dissolution suggests that this trend reflects in-lake production, and not water column or sedimentary diagenesis. Sedimentary OM was primarily of aquatic origin, as indicated by low C:N signatures (9.7–12.2; Meyers and Teranes 2001; Selbie et al. 2009; Fig. 4*a*). OM deposition trends were similar to those in inferred primary production ($BSiO_2$ flux, $r = 0.89$, $P < 0.0001$, $n = 45$), increasing coevally with regional warming (ca. mid-1800s; Table 2; Fig. 4*b*). Sedimentary $CaCO_3$ paralleled trends in OM sedimentation (% OM, $r = 0.75$, $P < 0.0001$, $n = 45$; Fig. 4*b*) and inferred primary production ($BSiO_2$, $r = 0.83$, $P < 0.0001$, $n = 45$), and was also strongly correlated to regional and pan-Arctic temperatures (Table 2).

Sedimentary diatom and cladoceran assemblages

The Tuya Lake diatom assemblage was dominated by planktonic species of high nutrient affinity (e.g., *Stephanodiscus minutulus/parvus* complex, *Asterionella formosa*, *Aulacoseira subarctica*) with lesser contributions from oligo-mesotrophic planktonic taxa (*Cyclotella ocellata* and *C. pseudostelligera*) and benthic taxa (Fig. 5; Cumming et al. 1995). DCA values indicated relatively stable species composition over much of the record (i.e., pre-20th century; Fig. 4*e*). Increases in *A. subarctica* abundance (larger, heavily-silicified morphotypes; Fig. 5) were generally consistent with regional warm periods during the latter Medieval Climate Anomaly (Hu et al. 2001; Wiles et al. 2004), a persistent warm PDO phase (ca. 1450–1550 AD; MacDonald and Case 2005), and the onset of regional warming in the ca. mid-1800s (Fig. 5). The most recent increase in *A. subarctica* marked the most pronounced diatom community change over the past millennium (DCA; Fig. 4*e*, Fig. 5), co-occurring with pronounced regional (BCMWLAP 2002) and global warming (Jansen et al. 2007), and a shift to a warm PDO regime in the Pacific Ocean in the late-1970s (Fig. 5; Mantua et al. 1997). The diatom species turnover from Tuya Lake was also nearly synchronous with millennially unprecedented climate change responses in the diatom communities of several northern Cordilleran lakes (Karst-Riddoch et al. 2005; Fig. 6).

The cellular morphology of *A. subarctica* varied markedly over the past millennium (valve diameter (D) = 3.11–12.22 µm; mantle height (H) = 3.08–18.77 µm). A distinct long and narrow, less-silicified morphotype, ($D_{mean} = 4.23 \pm 0.65$ µm (1 SD); $H_{mean} = 12.99 \pm 2.07$ µm (1 SD), $H{:}D_{mean} = 3.1$, $n = 500$) was rare over most of the record, consistent with its occurrence in most natural populations (Fig. 7*d*; Jewson 1992; Gibson et al. 2003). This morphotype increased substantially following the ca. mid-1800s, strongly correlated with inferred lake production and organic matter sedimentation (%OM, $r = 0.93$, $P < 0.0001$, $n = 25$; $\%N_{sed}$, $r = 0.80$, $P < 0.0001$, $n = 25$; $\%C_{sed}$, $r = 0.86$, $P < 0.0001$, $n = 25$; $CaCO_3$, $r = 0.83$, $P < 0.0001$, $n = 25$; $BSiO_2$, $r = 0.87$, $P < 0.0001$, $n = 24$), and regional and pan-Arctic temperatures (Table 2). Increases in the narrow *A. subarctica* morphotype co-occurred with warm PDO regimes in the Pacific Ocean, and the introduction of sockeye salmon ca. 1991 (Fig. 7*d*). Over the course of the past century, *A. subarctica* shifted to cell sizes at or below the limits for sexual reproduction reported in the literature (Jewson 1992; Gibson et al. 2003; Figs. 7*a*–7*c*).

Tuya Lake cladoceran zooplankton fluxes were low over most of the past ~1000 years (Fig. 4*d*). Prior to the 20th century, the community was dominated by benthic taxa (*Chydorus*, *Acroperus*, *Alona*, and *Eurycercus* spp.; Fig. 5). Notable community restructuring occurred with regional warming

Fig. 2. The radioisotopic (^{210}Pb, ^{14}C) age model for gravity core SG1–2003 from Tuya Lake, British Columbia, Canada. (*a*) Sedimentary ^{210}Pb activities with depth. The broken line indicates supported ^{210}Pb (background) as estimated by ^{214}Bi. (*b*) Comparison of sediment cumulative dry mass versus log-unsupported ^{210}Pb activity indicating negligible sediment disturbance. (*c*) Sediment core age-depth model based on a 2nd order polynomial fit through the core top (2003), ^{210}Pb dates (CRS model, filled circles, standard error shown) and a basal ^{14}C date (open circle, 2σ error). The broken line indicates the age-depth series based upon linear extrapolation of ^{210}Pb dates alone, which is in general agreement with our age model.

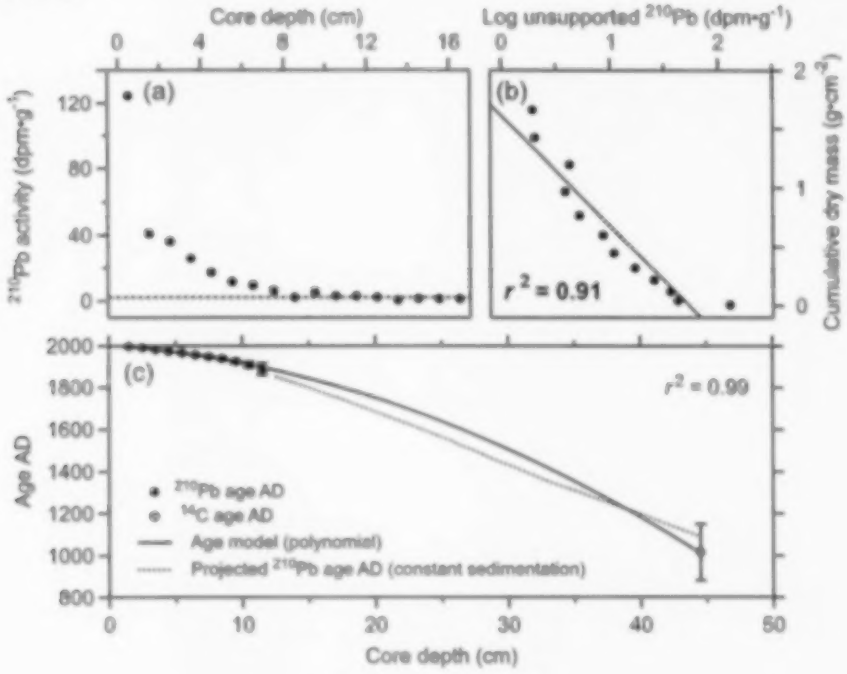


Fig. 3. The multicentennial δ^{15}N time series from Tuya Lake, British Columbia (BC), compared with published sockeye nursery lake isotope records from Karluk and Akalura lakes, Alaska (AK) (Finney et al. 2002), Nerka Lake, Alaska (Schindler et al. 2005), and Redfish Lake, Idaho (ID) (Selbie et al. 2007). The broken line indicates the mean δ^{15}N signature of surface sediments across 100 lakes (coastal and interior) in British Columbia and Alaska where sockeye salmon had not been introduced (nonsalmon lakes) (Selbie et al. 2009). A comparison of sedimentary δ^{15}N signatures from Tuya Lake, B.C., in relation to salmon and nonsalmon lakes in Pacific North America reveals depleted values more similar to nonsalmon systems than those receiving salmon-derived nutrients. In agreement with fisheries assessments (e.g., PSC 1988), the lack of enrichment in sedimentary δ^{15}N suggests Tuya Lake was likely devoid of spawning sockeye salmon over at least the past 1000 years.

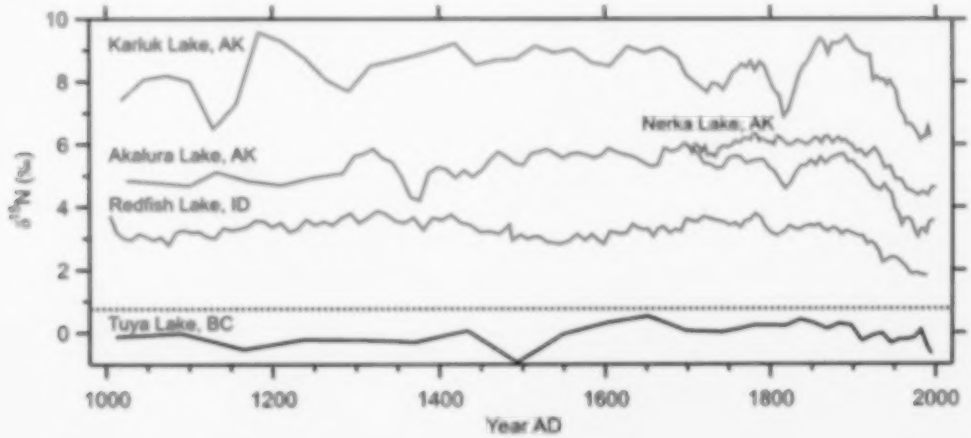


Fig. 4. Millennial time series of (*a*) carbon:nitrogen (C:N) ratio, (*b*) % organic matter, % carbonate; (*c*) planktonic:benthic (P:B) cladocera ratio; (*d*) biogenic silica and cladoceran fluxes; and (*e*) species turnover in cladoceran in diatom communities from Tuya Lake demonstrating marked post-1850 change. Also shown are correlated trajectories in (*f*) regional temperatures from northwest Canada (NWC) (Szeicz and MacDonald 1995), the Wrangell Mountains (WM), Alaska (Davi et al. 2003), the Rocky Mountains, British Columbia (Luckman and Wilson 2005); and (*g*) pan-Arctic temperatures (Overpeck et al. 1997). Annually resolved tree-ring reconstructions were averaged to time interval integrations in the Tuya Lake record. Vertical shaded areas represent warm/positive (light grey) and cold/negative (dark grey) phase shifts in the Pacific Decadal Oscillation (PDO; Mantua et al. 1997). The vertical broken line represents ca. 1991, the onset of salmon stocking in Tuya Lake.

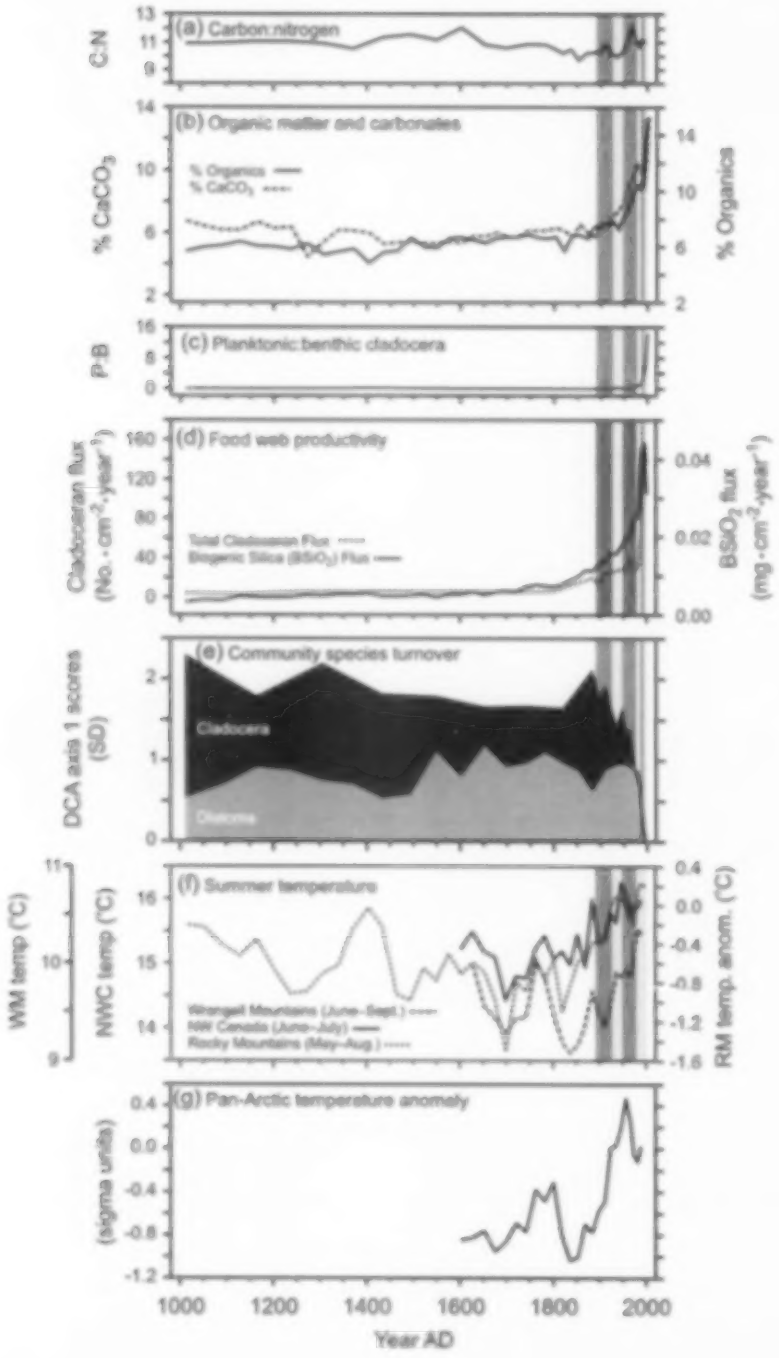


Table 2. Pearson correlations (r) for comparisons of Tuya Lake proxy data with regional and pan-Arctic temperature reconstructions.

	NW Canada temperature (Szeicz and Macdonald 1995)	n	Wrangell Mountain temperature (Davi et al. 2003)	n	Rocky Mountain temperature (Luckman and Wilson 2005)	n	Arctic temperature (Overpeck et al. 1997)	n
Organics (%)	0.71**	24	0.72**	25	0.70**	44	0.83**	25
Carbonate (%)	0.71**	24	0.69**	25	0.54**	44	0.73**	25
$BSiO_2$ flux	0.71**	24	0.69**	25	0.69**	44	0.75**	25
N_{tot} (%)	0.87**	19	0.80**	20	0.70**	30	0.84**	20
C_{tot} (%)	0.89**	19	0.80**	20	0.72**	30	0.87**	20
A. subarctica, narrow morph	0.79*	13	0.84**	14	0.74**	24	0.84**	14

Note: *A. subarctica*, *Aulacoseira subarctica*; significance levels (P values) represent Bonferroni-adjusted probabilities: **, $P < 0.01$; *, $P < 0.05$; all relationships were positive; transformations (%OM, log; %carbonate, log; $\%N_{tot}$, log; $\%C_{tot}$, log; *A. subarctica* narrow morph, square root; climate variables not transformed); annually resolved dendroclimatic time series (Szeicz and MacDonald 1995; Davi et al. 2003; Luckman and Wilson 2005) were averaged to the time intervals represented in the Tuya Lake sedimentary record prior to analysis.

(DCA; Fig. 4*c*), marked by initial increases in benthic species fluxes followed by millennially unprecedented fluxes of planktonic species over the 20th century (Figs. 4*c* and 5). Cladoceran productivity in Tuya Lake increased 20-fold over the period of warming (since ca. mid-1800s), consistent with the changes in inferred primary production (Fig. 4*d*).

Following the introduction of sockeye salmon to Tuya Lake (ca. 1991), inferred algal production ($BSiO_2$ flux) declined (29%; Fig. 4*d*). The diatom community composition remained dominated by *A. subarctica* (Fig. 5). Post-stocking cladoceran fluxes initially increased, but were followed by declines (Fig. 4*d*), consistent with monitoring observations (e.g., initial small-bodied *Daphnia* and *Bosmina* increases and subsequent loss of *Daphnia*; Mathias 2000; Fig. 5).

Modeled salmon biomass production, nutrient fluxes, and relationships to limnological and short-term climate variability

Annual sockeye salmon fry additions to Tuya Lake from 1991–2004 varied substantially (0–4.7 × 10^6 fish). Our population model estimated an annual smolt emigration of 2.10 × 10^4 – 1.06 × 10^6 fish, constituting 781.52–1.83 × 10^3 kg in biomass. Our age-structured mass balance model estimated that smolt emigration resulted in net exports of 2.0–78.3 kg P and 8.2–452.2 kg N annually over the study period (Fig. 8*a*). Estimated salmon biomass nutrient exports were capable of only minor euphotic zone nutrient reductions (6.88 × 10^{-3} – 0.28 μg·L^{-1} P and 0.03–1.59 μg·L^{-1} N), given the large pelagic area of Tuya Lake (Fig. 8*b*). Moreover, even at theoretical out-migrant densities equivalent to hydroacoustically derived fry abundances during the summer prior to outmigration (i.e., no overwinter mortality; +40% fish), lake nutrient reductions from this mechanism would likely only be minor (<0.5 μg·L^{-1} P and < 2 μg·L^{-1} N).

Substantial variation was observed in epilimnetic late-summer total phosphorus (LS TP; 8.4–14.0 μg·L^{-1}), dissolved inorganic nitrogen (LS DIN; 92.1–230.0 μg·L^{-1}), and chlorophyll (LS chl *a*; 1.0–3.0 μg·L^{-1}) over the monitoring period (1987–2003; Fig. 8*e*). Post-stocking LS TP, LS DIN, and LS chl *a* values were consistently lower than those measured prior to fish stocking (Table 1; Fig. 8*e*). LS TP was strongly and negatively correlated with estimated salmon biomass at outmigration the following year (r^2 = 0.87, P = 0.002; Fig. 8*c*), a temporal offset consistent with intensive foraging and biomass accumulation during the year prior to outmigration. Continuous LS TP values reconstructed from this empirical relationship and observed values were lower than pre-introduction LS TP values at all stocking densities, but approached pre-disturbance values during years when no fish were stocked (Fig. 8*e*). Owing to insufficient nitrogen monitoring data, a linear model, while demonstrating a strong negative relationship with modeled salmon biomass (r^2 = 0.83) lacked statistical power (P = 0.27) for similar DIN reconstructions. All observed LS DIN values were substantially lower than pre-stocking concentrations. Consistent with the LS TP – salmon biomass relationship, LS chl *a* varied strongly but positively with modeled salmon biomass the following year (r^2 = 0.87, P = 0.006) reflecting limnological responses during the pre-outmigration intensive foraging period (Fig. 8*d*). Reconstructed and observed post-introduction LS chl *a* concentrations were consistently much lower than the pre-disturbance values (Fig. 8*e*). Our survey data from 2003 indicated that LS chl *a* was dominated by N-fixing cyanobacteria (heterocystous *Anabaena* spp.) and colonies of the diatom *A. subarctica*. Neither LS TP nor LS chl *a* were significantly correlated to late-summer or annually averaged air temperatures (mean, minimum, maximum) or precipitation (rain, snow, total), consistent with a general inertial insensitivity of large lakes to short-term climatic fluctuations (Choi 1998).

Discussion

A pre-disturbance ecosystem context: multicentennial ecological stability in Tuya Lake

In agreement with pan-Arctic (Smol et al. 2005) and Northern Hemisphere (Rühland et al. 2008) lake responses to climate change, our multiproxy paleolimnological record revealed that modern (ca. post-1850) ecosystem conditions are fundamentally different from those over most of the past millennium. Autecological data for the dominant diatom species indicate that Tuya Lake has been persistently nutrient-rich (Kilham et al. 1996; Interlandi et al. 1999), yet inferred lake productivity has been low and algal community variation minimal until the 20th century implying, relative ecological stability over most of the record. Algal trends were mirrored by low cladoceran productivity, dominated by benthic taxa, and similar to pre-warming subarctic zooplankton communities at other sites (Korhola et al. 2002; Smol et al. 2005), probably reflecting inadequate conditions for pelagic

Fig. 5. The dominant diatom (>5% relative abundance, black) and cladoceran (all taxa, grey) community compositions in Tuya Lake over the past millennium. Benthic diatom taxa are presented as a total sum. Horizontal shaded areas represent warm/positive (light grey) and cold/negative (dark grey) phase shifts in the Pacific Decadal Oscillation (PDO) from the instrumental record (Mantua et al. 1997), tree-ring reconstructions (ca. 1450–1550 AD and ca. 1600–1800 AD; MacDonald and Case 2005), as well as the termination of the Medieval Climatic Anomaly (ca. 1000–1200 AD light grey gradation; Hu et al. 2001). The horizontal broken line represents ca. 1991, the onset of sockeye salmon stocking in Tuya Lake.

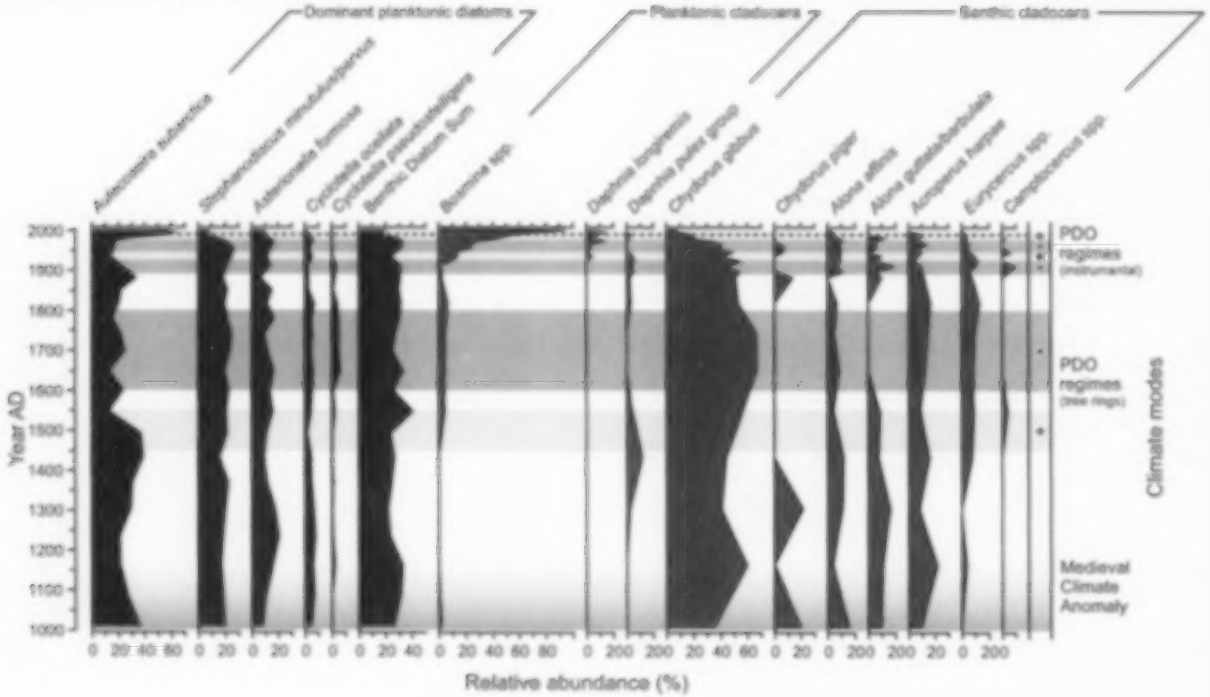
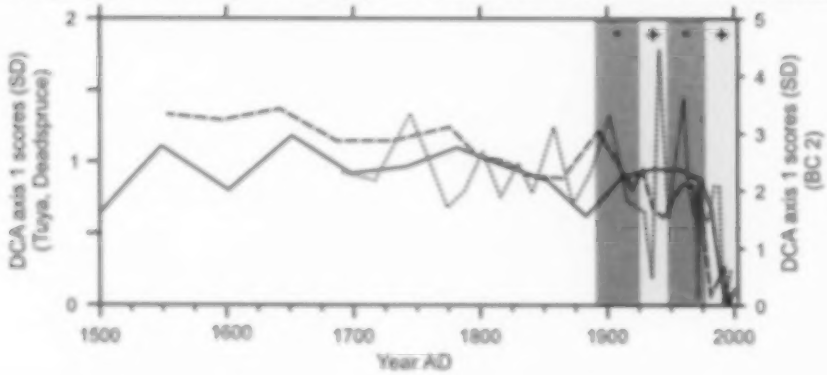


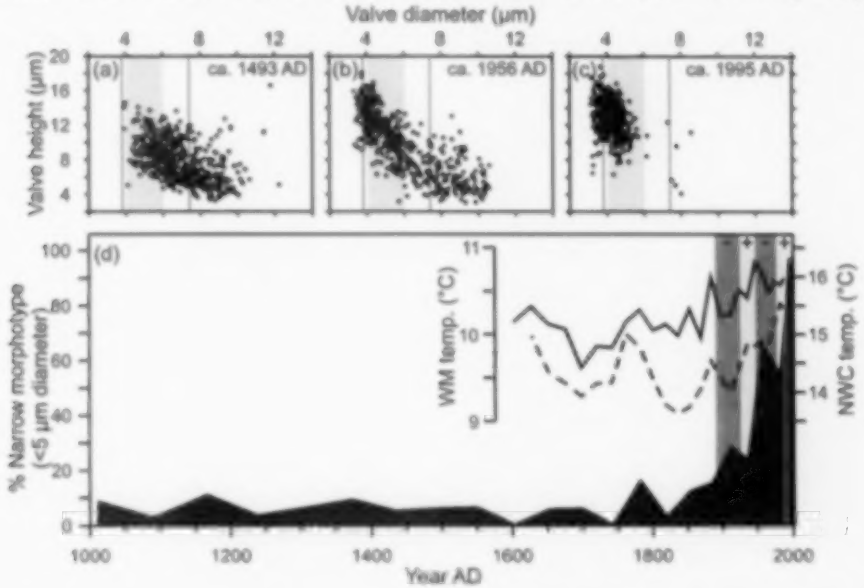
Fig. 6. Northern Cordilleran diatom community species turnover over the past ca. 500 years from Tuya (unbroken line), Deadspruce (dashed line), and BC2 lakes (dotted line; Karst-Riddoch et al. 2005), demonstrating pronounced change following the ca. late-1970s. Vertical shading represents warm/positive (light grey) and cold/negative (dark grey) modes of the Pacific Decadal Oscillation (PDO; Mantua et al. 1997).



community development (e.g., low temperatures, longer ice cover and shorter growing seasons, reduced pelagic forage; Korhola et al. 2002). Also consistent with this interpretation, regional and pan-Arctic paleoclimate records indicate the ecological stability in Tuya Lake coincided with the Little Ice Age, a period of persistently cold temperatures (Overpeck et al. 1997; Hu et al. 2001; Wiles et al. 2004).

Minor deviations from ecosystem stability in Tuya Lake were associated with periods of regional warming (e.g., the Medieval Climate Anomaly, warm Pacific Decadal Oscillation (PDO) events). The expansion of the broader, heavily-silicified morphotype of the diatom *Aulacoseira subarctica* during these periods may mark moderate reductions in seasonal ice cover and enhanced seasonal mixing (Gibson et al. 2003; Rühland et al. 2008), typical lake responses to warmer climates that stimulate algal production and species turnover

Fig. 7. Observed cellular morphological changes in the diatom *Aulacoseira subarctica* over the past millennium, highlighting trends towards narrower, longer cells after the ca. mid-1800s. Scatter plots ($n = 500$) demonstrate changes in population size structure during (*a*) the pre-disturbance period (ca. 1493 AD), (*b*) the period of climate warming (ca. 1956 AD) and (*c*) following sockeye salmon introductions (ca. 1995 AD). The minimum sexually inducible valve diameter ranges for *A. subarctica* reported in the literature by Jewson (1992) and Gibson et al. (2003) are delineated by grey shading and broken lines, respectively. Panel (*d*) denotes the percentage of total *A. subarctica* cells represented by the narrow, long morphotype (<5 μm diameter). Tree-ring reconstructions of summer temperature in NW North America (Szeicz and MacDonald 1995; Davi et al. 2003) are inset for comparison. Climatic time series are averaged to time interval integrations in the Tuya Lake record. Vertical shaded areas represent warm/positive (light grey) and cold/negative (dark grey) phase shifts in the Pacific Decadal Oscillation (PDO; Mantua et al. 1997). The white vertical broken line denotes ca. 1991, the onset of sockeye salmon stocking in Tuya Lake.



at high latitudes (Douglas et al. 2004; Smol et al. 2005; Smol and Douglas 2007). The modest development of planktonic cladoceran communities (e.g., *Daphnia pulex* group, *Bosmina* spp.) during these intervals suggests broader food web responses to past warming (Korhola et al. 2002).

Overall, our paleolimnological record captured muted productivity and ecological variation in Tuya Lake prior to the mid-1800s. These trends were consistent with subtle regional climate variation over this period (Hu et al. 2001), and complacent diatom variation in other remote northern Cordillera lakes attributed to enhanced ice cover associated with the Little Ice Age (Karst-Riddoch et al. 2005).

"Ecosystem climate conditioning": recent warming influences on lake ecology

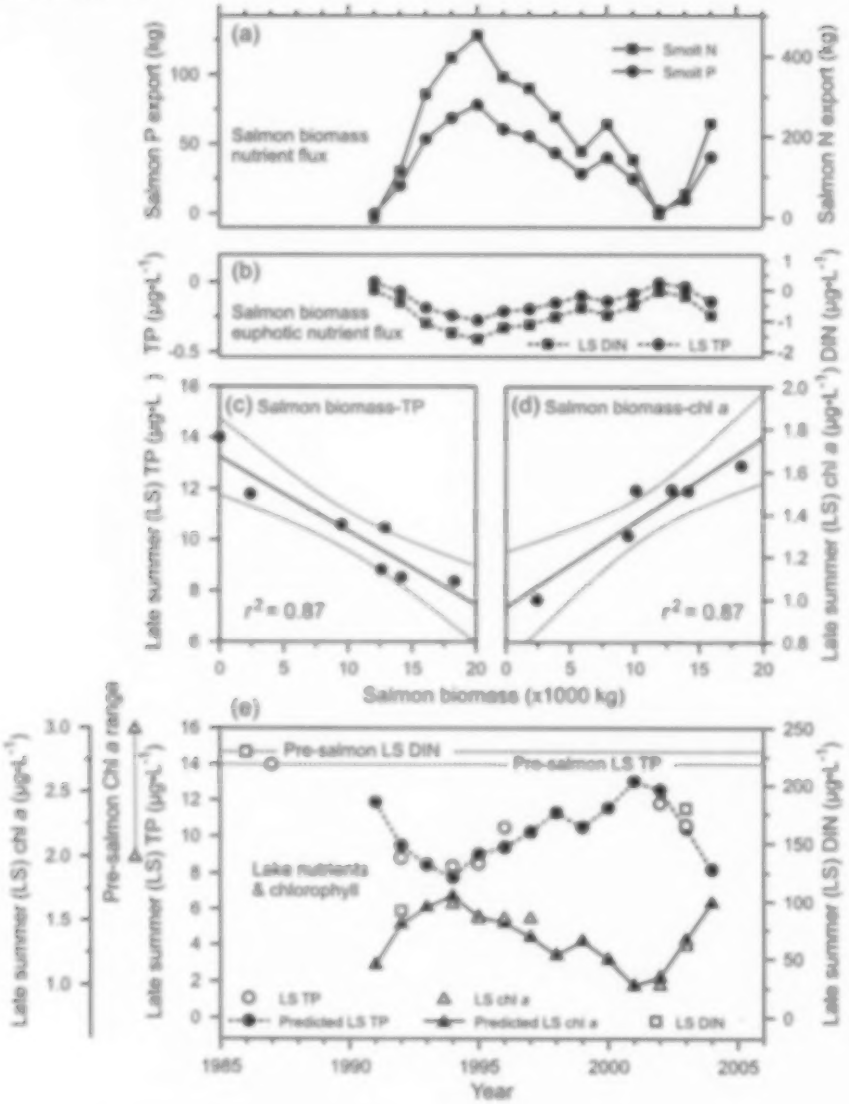
Monitoring (IPCC 2007) and predictive modeling (Giorgi 2006) purport northwestern North America, especially the northern Cordillera (BCMWLAP 2002; Diaz et al. 2006), to be a global climate change "hot spot," an assertion supported by regional paleoclimatic reconstructions tracking pronounced warming since ca. mid-1800s. Available evidence indicates that northern Cordilleran lakes have exhibited strong physical, chemical, and biological responses to this recent warming (BCMWLAP 2002; Karst-Riddoch et al. 2005).

Given its subalpine and subarctic position, elevated nutrient status, and pronounced regional warming, we expected Tuya Lake to be ecologically sensitive to climate change. The strong correlations between independent proxies of primary production, autochthonous organic matter sedimentation, and regional and pan-Arctic temperatures support these predictions, highlighting a strong link between lake productivity and recent climate change. Commensurate restructuring of algal and zooplankton communities and the millennially unprecedented 20th century shift towards a productive pelagic food web contrasted with previously muted ecosystem variability, but was consistent with typical northern and alpine lake responses to climate warming (Hauer et al. 1997; Rouse et al. 1997; Smol et al. 2005). In light of the remoteness of Tuya Lake (e.g., negligible human disturbances), we conclude that climate warming was most likely the principal forcing behind the ecological changes observed following the ca. mid-1800s.

The mechanisms underlying remote northern and high-altitude lake ecosystem responses to climate change can be complex and interactive, involving both lakes and their watersheds (Schindler 1997). For instance, warming can increase lake productivity via enhanced watershed biogeochemical cycling and nutrient delivery (Hauer et al. 1997; Rouse et al. 1997). While a possible contributing factor to the production increases in Tuya Lake, low food web productivity over the past millennium, despite diatom-inferred persistence of nutrient-rich conditions, suggests increased nutrient loading was not a primary control on lake productivity.

Alternatively, climate-mediated changes in light-attenuating dissolved organic carbon (DOC) could have influenced lake production through variations in water column light penetra-

Fig. 8. Monitoring and modeled time series of introduced salmon biomass production, lake nutrients, and algal production in Tuya Lake, British Columbia. (*a*) Modeled salmon biomass-mediated nutrient (phosphorus and nitrogen) fluxes; (*b*) Estimated euphotic nutrient fluxes resulting from salmon biomass fluxes; (*c*) Empirical relationship between modeled salmon biomass exports and late-summer total phosphorus (TP) the year prior to outmigration. Broken curves indicate 95% confidence intervals. (*d*) The empirical relationship between modeled salmon biomass exports and late-summer chlorophyll *a* the year prior to outmigration. Broken curves indicate 95% confidence intervals. (*e*) Measured and reconstructed TP and chl *a* time series. Reconstructions are based upon models developed in (*c*) and (*d*). Horizontal broken lines indicate pre-introduction levels of TP and dissolved inorganic nitrogen, DIN (Coombes 1986). The pre-introduction growing season chl *a* range (PSC 1994) is shown as a vertical broken line.



tion (DOC; Morris et al. 1995; Pienitz and Vincent 2000; Leavitt et al. 2003). Lake DOC varies with catchment arboreal vegetation (e.g., Leavitt et al. 1997; Pienitz and Vincent 2000), and as Tuya Lake lies on the altitudinal ecotone bordering subalpine coniferous forest and tundra, elevation of treeline may have occurred with warming, increasing lake DOC and productivity via ultraviolet radiation (UVR) inhibition release. Although the lack of long-term watershed vegetation data precludes examination of this effect on past lake productivity, the moderate DOC levels in Tuya Lake at present indicate that warming-mediated DOC increases, if any, have been modest. Additionally, no temporal lag occurred between warming and the increases in lake production as would be expected given terrestrial vegetation colonization and growth delays, suggesting DOC was unlikely a first-order driver of the food web productivity changes in Tuya Lake.

DOC can, however, influence seasonal stratification patterns and mixing depths (Cahill et al. 2005), which may have indirectly contributed to the lake production responses.

The seasonal extent and timing of ice and snow cover are dominant controls on lake physics and productivity in northern and alpine regions (Douglas et al. 2004; Karlsson et al. 2005; Smol and Douglas 2007). Warming air temperatures reduce seasonal ice cover, enhancing lake production via longer insolation periods, earlier and prolonged stratification (De Stasio et al. 1996; Cahill et al. 2005; Rühland et al. 2008), and deeper mixed layers (Rouse et al. 1997; Cahill et al. 2005). Warming impacts on freeze–thaw dynamics have been detected in lakes of the northern Cordillera (Karst-Riddoch et al. 2005), where warming has advanced snow melt by 9 days·decade^{-1} and ice-off on lakes by 3 days·decade^{-1} over 52 years (BCMWLAP 2002). Although the instrumental record partially reflects regional climate variability (i.e., Pacific Decadal Oscillation), changing ice cover has likely significantly influenced Tuya Lake over the instrumental record (i.e., predicted snow melt up to 1.6 months earlier and ice-off up to 0.6 months earlier) with probably larger changes since the onset of climate warming.

Given the trophic status of Tuya Lake and its limited modern ice-free period (4–5 months), even modest changes in ice cover could have elicited pronounced physical and biological responses. Early (ca. late-1800s) increases in broader, heavier-silicified forms of *A. subarctica* were analogous to those during prior warm periods, possibly reflecting seasonal advancement of ice-free conditions. Replacement of *A. subarctica* by stratification-tolerant species (e.g., *Stephanodiscus minutulus/parvus*, *Asterionella formosa*; Kilham et al. 1996), coupled with increases in inferred primary productivity, support a development and intensification of lake stratification. Similar trends in cladoceran production, marked by initial increases in benthic taxa followed by a millennially unprecedented transition (ca. early-1900s) to planktonic species (e.g., *Bosmina* spp., *Daphnia* spp.), represent typical responses to warming and enhanced stratification (e.g., Korhola et al. 2002; Smol et al. 2005), and corroborate a co-development of water column stability and pelagic food web production with warming. Trends in sedimentary carbonate ($CaCO_3$), also support warming-enhanced stratification. Strongly correlated with regional and pan-Arctic temperatures, the doubling of $CaCO_3$ since the ca. mid-1800s is consistent with increased autochthonous $CaCO_3$ production resulting from primary producer carbon dioxide removal from an increasingly stratified water column (e.g., Reynolds 1976; Schelske and Hodell 1991). Our limnological data support this interpretation, as marked vertical pH structure develops in the modern stratified water column (alkaline epilimnion, circumneutral hypolimnion), with pH positively correlated to water temperature ($r = 0.99$, $P < 0.0001$, $n = 36$) and dissolved oxygen ($r = 0.98$, $P < 0.0001$, $n = 36$) likely reflecting epilimnetic productivity.

The unique cellular size reductions in the diatom *Aulacoseira subarctica* in Tuya Lake were strongly correlated to regional and pan-Arctic air temperatures, as well as lake productivity and organic matter sedimentation proxies, providing additional support for an enhancement of stratification and productivity with climate warming. Earlier and stronger stratification imposes significant chemical (e.g., seasonal epilimnetic nutrient restrictions) and physical stresses (e.g., sedimentation losses) on trophogenic populations of heavily silicified *Aulacoseira* species (Reynolds 1994). The morphological changes in *A. subarctica* differed from *Aulacoseira* (*Melosira*) responses to silica limitation (Stoermer et al. 1985), but were consistent with adaptations reducing planktonic diatom sedimentation losses (e.g., reduced size and silicification, higher surface area to volume ratio; Smol et al. 1984), differential sinking rates of *Aulacoseira* cells (Davey 1986), and proliferation of smaller planktonic diatoms with warming (Rühland et al. 2008; Winder et al. 2009). Thus, the shift to longer, narrower cells may have been an adaptive antisedimentation response to increasing water column stability. This is consistent with the ecology of *A. subarctica* in large lakes, where it can persist throughout stratification in metalimnetic or upper-hypolimnetic populations (Kilham et al. 1996; Interlandi et al. 1999), facilitated by a low light tolerance (Kilham et al. 1996; Gibson et al. 2003).

The pronounced ecosystem changes observed in Tuya Lake following the 1970s were nearly synchronous with species turnover in the diatom communities of several remote northern Cordilleran lakes. These changes were coeval with enhanced regional- (BCMWLAP 2002) and global-scale warming (Jansen et al. 2007) and a warm PDO regime shift in the Pacific Ocean (Mantua et al. 1997), possibly reflecting ecological responses to interactive climate processes as has been observed at temperate latitudes (Winder and Schindler 2004). Diatom species turnover in Tuya Lake was marked by substantial increases in *A. subarctica* (long, narrow morphotype), and declines in stratification-tolerant diatoms (e.g., *A. formosa*, *S. minutulus/parvus*), which contrasted with earlier trends and autecological predictions of species responses to enhanced stratification (Kilham et al. 1996; Gibson et al. 2003; Rühland et al. 2008). Given the strong modern stratification in Tuya Lake and the coherent diatom responses across several disparate northern Cordilleran lakes (i.e., climate forcing), the post-1970s diatom shifts implicate the development of a secondary climate-mediated stressor on Tuya Lake.

Seasonal epilimnetic nutrient restrictions are expected to have accompanied the exceptional post-1970s increases in stratification and productivity in Tuya Lake. Millennially unprecedented increases in *A. subarctica* abundance contrasted with expected responses to warming in Northern Hemisphere lakes (i.e., declines in *Aulacoseira* species; see Rühland et al. 2008), and occurred against strong physiological (e.g., lower nutrients and light; enhanced sedimentation losses due to stratification) and life history stresses (e.g., vegetative persistence beyond sexually inducible sizes), implying a strong competitive advantage for this species under warming. *Aulacoseira subarctica* outcompetes *S. minutulus* and *A. formosa* under low N and low light conditions (Kilham et al. 1996; Interlandi et al. 2003), and can proliferate under epilimnetic N-limitation in deepwater populations (Interlandi et al. 1999, 2003). As such, coupled with the potential antisedimentation response, we interpret the post-1970s expansion of *A. subarctica* to reflect the development of seasonal N-deficits arising from enhanced lake stratification and productivity. This inference is supported by the development of modern N-deficits in Tuya Lake as evidenced by lower than expected pre-stocking algal production given ambient P levels (PSC 1994), late-

summer sestonic stoichiometry (molar POC:PON) indicating N-limitation (Table 1; Hecky et al. 1993), and the dominance of the late-summer algal guild by N-fixing cyanobacteria (heterocystous *Anabaena* spp.) and *A. subarctica*.

Seasonal N-deficits in Tuya Lake likely resulted from enhanced sedimentation losses of biologically sequestered nutrients as lake stratification developed with warming. A principal nutrient loss pathway in dimictic lakes (Vanni 2002; Sommer and Sommer 2006), increased herbivory, as likely accompanied the 20-fold increases in pelagic cladoceran productivity in Tuya Lake over the past century, increases vertical nutrient losses in mesotrophic systems (Houser et al. 2000; Vanni 2002). Such losses occur via increased algal sinking rates, size-selective grazing (Mazumder et al. 1989), aggregation of nutrients in fast-sinking fecal pellets (Bloesch and Bürgi 1989), and senescent zooplankton biomass losses (Houser et al. 2000). Given the large, deep pelagic zone of Tuya Lake such permanent loss processes were probably important in reducing euphotic nutrient availability with warming.

Overall, the synchrony of ecological changes in Tuya Lake following the mid-1800s (e.g., lake stratification and food web productivity increases, community composition, and species life history changes) with northern climate warming and ecosystem changes in other Cordilleran lakes, indicate that climate change has greatly altered the structure and functioning of the Tuya Lake ecosystem. In the context of the past millennium our data reveal a complex ecosystem "climate conditioning" that exceeded the influences of natural climatic variability (Hu et al. 2001).

Ecological impacts from salmon introduced to a "climate-conditioned" ecosystem

Our paleoecological record from Tuya Lake demonstrates that sockeye salmon were introduced to a nursery ecosystem fundamentally altered by the effects of climate warming. We hypothesized that the structural and functional ecosystem changes and sensitivities (e.g., lake stratification, enhanced pelagic productivity, N-deficits) induced by climate change would influence the nature and extent of ecosystem impacts arising from salmon rearing in Tuya Lake.

Comparisons between our limnological time series and our fisheries models revealed that nutrient availability in Tuya Lake varied strongly and inversely with salmon biomass production. Late-summer (LS) epilimnetic total phosphorus (TP) and dissolved inorganic nitrogen (LS DIN) concentrations were substantially depleted relative to pre-stocking levels (mean LS TP = –4.2 $\mu g \cdot L^{-1}$, mean LS DIN = –94.0 $\mu g \cdot L^{-1}$), and LS TP was negatively correlated ($r^2 = 0.87$) to modeled outmigrating salmon biomass. The temporal offset in this correlation was consistent with foraging and biomass accumulation the year prior to outmigration, and a typical one year freshwater residence for Tuya Lake juvenile sockeye salmon. Residualized sockeye salmon (i.e., kokanee) in Tuya Lake (Beere 2002) may have contributed to the observed nutrient reductions; however, the majority of the variation in nutrient availability (87% of LS TP) is explained by anadromous sockeye biomass production. The domination of the LS phytoplankton by low-N-tolerant algal taxa (N-fixing cyanobacteria, *Aulacoseira subarctica*), coupled with sizeable post-stocking LS DIN reductions, and persistent P availability throughout the growing season suggest that salmon have most greatly reduced seasonal N availability in Tuya Lake.

While introduced planktivores can elicit cascading grazing effects on phytoplankton (i.e., stimulation of algae via enhanced nutrient cycling; Carpenter and Kitchell 1993), the post-stocking declines in LS chl *a*, and commensurate decreases in sedimentary algal fluxes, suggest that introduced salmon limited, rather than stimulated algal productivity in Tuya Lake. Insufficient temporal resolution in the nutrient data limit our assessment of seasonal nutrient deficiencies arising from the salmon introductions, but it is possible that enhanced nutrient cycling, which can scale with introduced planktivore biomass (Schindler et al. 2001), stimulated early season productivity, reducing total primary production through earlier induction of N-deficiencies.

The strong positive correlation linking salmon biomass production to LS chl *a* ($r^2 = 0.87$) initially appeared to contrast with our limnological and paleolimnological evidence for N-limitation of algal production in Tuya Lake. However, given the substantial reductions in post-stocking total algal production, and the domination of LS phytoplankton by low-N-tolerant species (heterocystous *Anabaena* spp., *A. subarctica*), we interpret this relationship to reflect LS increases in N-fixing cyanobacteria in response to salmon-mediated N-deficits.

Moore and Schindler (2004) predicted that in barren lakes stocked with sockeye salmon, outmigrating smolts act as net exporters of lake nutrients through biomass-sequestered nutrient losses. Our mass balance models support this hypothesis, estimating net salmon-mediated nitrogen (up to 452 kg $N \cdot year^{-1}$) and phosphorus (up to 78 kg $P \cdot year^{-1}$) exports in all years following stocking. Our volumetric calculations, however, revealed these losses were minor in Tuya Lake relative to its large euphotic volume. Thus, the salmon-mediated reductions in nutrient availability were not fully attributable to biomass exports, an interpretation that is upheld even when more liberal upper estimates of smolt production from available salmon fry hydroacoustic surveys were considered (e.g., +40%, K.D. Hyatt, unpublished data). Additional loss processes must have contributed to the salmon-mediated nutrient reductions in Tuya Lake.

Enhancement of epilimnetic loss processes (i.e., sedimentation during stratification) likely accompanied the salmon introductions, as simple biomass nutrient sequestration by algae or zooplankton cannot fully explain the LS TP depletion (i.e., TP integrates dissolved and biologically attenuated P pools). Mathias (2000) highlighted that salmon stocking did not reduce total zooplankton biomass in Tuya Lake, but caused notable trophic restructuring that could have influenced nutrient availability. Cladoceran zooplankton (primarily *Bosmina* spp.) increased substantially following stocking (Mathias 2000). This response may reflect a predation release, as introduced sockeye fed selectively, rapidly excluding large predatory copepods (e.g., *Epischura*, *Heterocope*; Mathias 2000). However, the observed shift towards a small-bodied zooplankton community (e.g., *Bosmina* spp.) is a typical compensatory response to enhanced zooplanktivory (Brooks and Dodson 1965). The resultant shift in zooplankton grazing habits from greater omnivory (large calanoid copepods) to increased herbivory (primarily *Bosmina* and to a lesser extent small-bodied *Daphnia* spp.), may have substan-

tially increased losses of euphotic N and P through biomass sequestration (Sommer and Sommer 2006) and sedimentation exports (Houser et al. 2000; Vanni 2002; see previous climate discussion). Moreover, such losses may have been accentuated by the LS algal shifts, as *Bosmina* has been shown to selectively feed on filamentous algae including *Aulacoseira* (*Melosira*) and *Anabaena* (Fulton 1988).

Our integration of fisheries modeling, monitoring, and paleolimnological data indicate that salmon introductions to Tuya Lake have reduced biological nutrient availability and primary productivity, with the most plausible mechanism being the enhancement of autotrophic N-deficiencies. As the seasonal N-deficits in Tuya Lake are an ecosystem sensitivity most likely induced by warming, our study reveals a modulation of the ecological effects of salmon stocking by climate change. Relative to the past millennium, sockeye salmon introductions likely would have elicited very different ecological responses in the absence of climate warming. However, given limited pelagic food web productivity, Tuya Lake likely would not have been an attractive candidate system for salmon introductions prior to warming.

Overall, our study establishes previously unconsidered and cryptic interactions of climate change and salmon introductions on lake structure and functioning, highlighting millennially unprecedented ecosystem responses to these compounding stresses. Our study supports previous research indicating substantial restructuring of sensitive northern lake ecosystems with warming (e.g., Smol et al. 2005; Rühland et al. 2008); however, our results document an ecosystem climate conditioning effect of warming that can modulate the ecological influences of subsequent stresses. In the context of predicted global temperature increases (IPCC 2007), and threshold responses in regional climatic and ecological systems (Walther et al. 2002; Smol et al. 2005), the effects of climate conditioning on aquatic ecosystems must be carefully weighed, as it may dictate the impacts of subsequent stresses. With declines in regional Pacific salmon production, the creation of supplementary terminal fisheries is an attractive management strategy, particularly in more pristine, northern lakes. Our results highlight unforeseen complexity in ecosystem responses, however, and echo a precautionary note, as stocking of non-native salmon in more typical, nutrient-poor coastal lakes may have untold and complex impacts on these ecosystems.

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The consequences of short-term cortisol elevation on individual physiology and growth rate in wild largemouth bass (*Micropterus salmoides*)

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Abstract: In this study, we explored the growth, survival, and potential population-level effects of short-term experimentally induced stress in largemouth bass (*Micropterus salmoides*). Cortisol implants [50 mg·(kg body mass)$^{-1}$] were used to increase circulating stress hormones in a group of wild fish in a research lake for ~6 d in June 2007. Through mark-and-recapture, we compared survival, growth, and plasma biochemistry of cortisol-treated, sham-treated, and control fish at liberty until October 2007. Cortisol-treated fish displayed persistent growth rate depression compared with other groups. However, neither plasma biochemistry nor mortality rates differed among treatments. In a complementary study, we found that the standard metabolic rates (SMR) of cortisol-treated fish were higher than control fish ~56 h following treatment. Bioenergetics modelling revealed that a transient elevation in SMR alone was insufficient to explain the observed growth depression. Finally, we constructed a simple population model to explore the potential consequences of growth depression. We found that a 10% reduction in population growth rate is conceivable when 39% of the population experiences a stress causing the growth rate depression documented in this study. Our study is novel in highlighting that individual and potentially population-level growth depression can result from a single stress event of short duration.

Résumé : Notre étude examine la croissance, la survie et les effets démographiques potentiels d'un stress à court terme provoqué expérimentalement chez l'achigan à grande bouche (*Micropterus salmoides*). Des implants de cortisol [50 mg·(kg de masse corporelle)$^{-1}$] ont servi à augmenter les hormones de stress en circulation chez un groupe de poissons sauvages dans un lac expérimental durant ~6 jours en juin 2007. Par marquage et recapture, nous avons comparé la survie, la croissance et la biochimie du plasma chez des poissons traités au cortisol, des poissons ayant reçu un traitement simulé et des poissons témoins jusqu'en octobre 2007. Par comparaison aux autres groupes, les poissons traités au cortisol accusent une dépression persistante de leur taux de croissance. Il n'y a cependant pas de différence dans la biochimie du plasma, ni dans la mortalité entre les traitements. Dans une étude complémentaire, nous avons observé que le taux métabolique standard (SMR) des poissons traités au cortisol était supérieur à celui des poissons témoins ~56 heures après le traitement. Un modèle bioénergétique montre qu'une élévation transitoire du SMR seule ne suffit pas à expliquer la dépression de la croissance observée. Nous avons enfin élaboré un modèle démographique simple pour examiner les conséquences de la dépression de la croissance. Il indique qu'il est concevable d'avoir une réduction de 10 % du taux de croissance de la population lorsque 39 % de la population encourt un stress provoquant une dépression du taux de croissance de l'ordre de celle observée dans notre étude. L'originalité de notre recherche est qu'elle souligne qu'une dépression de la croissance au niveau individuel et potentiellement à l'échelle de la population peut résulter d'un seul événement de stress de courte durée.

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Introduction

The endocrine stress response is an adaptive mechanism that promotes the survival and recovery of individuals during and after challenging events (Sapolsky et al. 2000; Greenberg et al. 2002). This response, characterized by the production and release of glucocorticoid hormones (Axelrod and Reisine 1984), is associated with a suite of secondary system-level and tertiary whole-animal changes that range from increases in carbohydrate catabolism to complex behavioural changes (Barton 2002). One of the primary adaptive roles of cortisol is the mobilization of energy reserves in response to stress (Van der Boon et al. 1991; Schreck et al. 1997; Wendelaar-Bonga 1997). Elevated cortisol is also associated with increases in aerobic and anaerobic metabolism (Morgan and Iwama 1996; De Boeck et al. 2001) and an increase in standard metabolic rate (Lankford et al. 2005). These changes serve to increase the energy immediately available for individuals to adequately respond to abiotic or biotic challenges (Barton 2002).

Elevated plasma cortisol is associated not only with the mobilization of energy reserves, but also with a reduction in feeding (Gregory and Wood 1999; Lankford et al. 2005). The relationship between foraging behaviour and stress has been explored in a wide variety of taxa using a range of stressful stimuli, and consistently links stress to a reduction in foraging (see reviews by Schreck et al. 1997; Carr 2002; Greenberg et al. 2002). For example, simulated trawling (Olla et al. 1997), environmental toxicants (McGeer et al. 2000), and salt stress (De Boeck et al. 2000) have been reported to reduce feeding behaviour in salmonids. In particular, food-searching behaviour is reduced in response to stress (Beitinger 1990), and in response to increased levels of predation (Gilliam and Fraser 1987; Abrahams and Sutterlin 1999). The proximate mechanism underlying the organismal changes in response to stress is uncertain, but evidence strongly supports the involvement of the hypothalamus–pituitary–interrenal axis (Bernier and Peter 2001), specifically cortisol and corticotropin-releasing factor (Bernier 2006). For example, administrations of exogenous cortisol (Gregory and Wood 1999) and corticotropin-releasing factor (De Pedro et al. 2003; Bernier and Peter 2001) have both been shown to decrease feeding in fishes in the laboratory. However, whether such mechanisms also operate in wild fish populations in situ has not yet been studied.

Although the cellular and organismal changes associated with a stress response are adaptive in the short term, these changes become maladaptive and are associated with decreases in somatic growth rate when circulating cortisol concentrations are chronically elevated (Gregory and Wood 1999; Edeline et al. 2009). For example, in goldfish (*Carassius auratus*), elevated cortisol has also been shown to reduce growth despite normal feeding behaviour (Bernier et al. 2004) indicating that there is a metabolic cost of stress. For wild fish, where animals rely on foraging success to recover energy stores lost during exposure to an acute stressor, and where anti-predator behaviour must be maintained to survive, reductions of individual growth rates may have important implications for survival and reproduction. For example, in males, larger individuals may be better competitors and attract more females (Foote 1988; Dunlop et al. 2007), and indeed larger male smallmouth bass (*Micropterus dolomieu*) are able to obtain more eggs to fertilize and guard than smaller males (Dunlop et al. 2007; Hanson and Cooke 2009). In females, fecundity is exponentially correlated with body size (Sargent and Gross 1986; Birkeland and Dayton 2005). Furthermore, fish size for both sexes can be correlated with overwinter survival in northern latitudes (Biro et al. 2004). Therefore, reductions in individual somatic growth rate can have a negative impact on reproduction and survival. While there have been laboratory studies that have confirmed costs to stress and extrapolated the results to wild animals (Edeline et al. 2009), it is unclear whether laboratory-assessed impacts of stress are relevant to wild fish populations.

In this study, we investigated the potential long-term (5 month) consequences of a transient (6 d) elevation of circulating cortisol in wild, free-swimming fish. We employed a mark-and-recapture approach to compare survival, growth rates, and plasma biochemical indices among largemouth bass (*Micropterus salmoides*) treated with an implant that raises circulating cortisol for ~6 d, sham-treated fish, and control fish at liberty over a 5 month period. Standard metabolic rate (SMR) measurements and bioenergetics modelling were employed to understand whether changes in metabolic rate could account for changes in growth rate. Finally, we constructed a simple population model to explore potential population-level consequences of short-term stress. The combination of experiments was aimed at exploring the long-term consequences of exposure to a transient cortisol elevation, identifying some of the potential regulating mechanisms, and exploring how these changes might affect wild fish populations.

Materials and methods

Long-term effects of transient plasma cortisol elevation in free-swimming wild fish

To study the long-term (5 month) costs of a short-term (6 d) cortisol elevation, we captured 207 mature (>250 mm) largemouth bass by rod-and-reel angling from Warner Lake, a small (8.2 ha surface area) private research lake in eastern Ontario (44°31′N, 76°22′W). To avoid any confounding effects of reproduction, initial treatment occurred between 24 and 28 June 2007, after the cessation of all spawning and parental care activities in this lake. Warner Lake is closed to immigration and emigration for fish, and fishing (including recreational angling) is prohibited aside from research purposes. All captured fish were landed within 20 s, and placed in a foam-lined trough that exposed the ventral side while keeping the gills submerged in fresh lake water. To establish baseline plasma biochemical parameters indicative of feeding and fasting (Congleton and Wagner 2006), approximately 1.5 mL of blood was withdrawn by caudal puncture into lithium-heparinized 3 mL vacutainer-style syringes (B.D., Franklin Lakes, New Jersey) from a random subset of animals. All fish were then scanned for a passive integrated transponder (PIT) tag (12.5 mm × 2.0 mm) using a PIT tag reader (Biomark, Boise, Idaho), and given a unique intracoelomic PIT tag if necessary. Warner Lake is a research lake, and fish have been PIT-tagged since 1993 for routine population monitoring. Of the 207 fish captured, 55 fish already carried PIT

tags. Fish were measured (total length, TL), and size-matched by TL into three treatment groups: cortisol, sham, or control (Table 1). Fish requiring new PIT tags were also distributed evenly among treatment groups. Cortisol-treated fish were injected with cortisol (hydrocortisone; Sigma H4001, Sigma-Aldrich Inc., St. Louis, Missouri) emulsified in coconut oil (*Cocos nucifera*; Sigma C1758, Sigma-Aldrich Inc.). Sham-treated fish were injected with pure coconut oil. Control fish were not injected. Cortisol was mixed with coconut oil at a constant ratio of 10 mg·mL^{-1}, and cortisol-treated fish were injected with the cortisol – coconut oil mixture based on body size at a dose of 0.005 mL·g^{-1}, leading to a final dose of 0.05 mg·g^{-1} based on fish mass. Sham-treated fish were injected with pure coconut oil at the same dose of 0.005 mL·g^{-1}. For all fish, body mass was estimated from a mass–TL relationship, (mass in g) $= (1.359 \cdot 10^{-4}) \cdot \text{TL in mm}^{2.998}$. This relationship ($R^2$ = 0.949) was previously developed from 68 mature largemouth bass captured between 2003 and 2006 in Warner Lake during the summer post-spawning period (i.e., June and July). All fish were released following treatment. Sexing largemouth bass externally is unreliable out of the breeding season, and so fish were not sexed, and were likely a mixture of males and females.

To monitor the fate and growth of the three treatment groups, between 20 and 25 August (i.e., 54 to 63 d following initial treatment), 206 mature largemouth bass were captured by rod-and-reel angling from Warner Lake, sampled for blood, measured (TL), and scanned with a PIT tag reader as described above. The process was repeated between 10 and 15 October (i.e., 105 to 114 d following initial treatment), when 151 mature largemouth bass were captured, sampled for blood, measured (TL), and scanned with a PIT tag reader.

All blood samples were held in water-ice slurries for no more than 1 h, until being centrifuged at 10 000*g* for 5 min (Compact II Centrifuge, Clay Adams, New Jersey). Plasma samples were flash-frozen in liquid nitrogen and stored at –80 °C until analysis.

Water temperatures were stable between 24 June and 25 August, ranging from 23 °C to 25 °C, with the highest temperatures occurring between 20 July and 10 August. After 25 August, water temperatures declined steadily through the fall, reaching 11 °C by 15 October.

Biochemical indices of fasting

To better appreciate the relevance of circulating plasma biochemical parameters assessed in the wild, 12 largemouth bass were captured by rod-and-reel angling from Lake Opinicon, a nearby public lake that is part of the Rideau River system in eastern Ontario (44°30′N, 76°20′W) from 15 to 19 June 2007. These fish were transported to the Queen's University Biological Station (on Lake Opinicon) in aerated coolers, where they were measured (TL), weighed, and size-matched by mass into two groups; fed and fasted fish (Table 1). Fish were anchor-tagged for individual identification, and then placed in two 750 L holding tanks with flow-through lake water, in mixed treatment groups (n = 3 from each treatment group in each tank; n = 6 fish per tank).

Starting on the day of capture, and every other day thereafter, fish in the fed treatment group were force-fed the equivalent of 2% of their body mass with a 1 g·mL^{-1} mixture

Table 1. Total length (TL in mm; mean ± SE; sample sizes are listed in parentheses) and mass (in g; mean ± SE; sample sizes are listed in parentheses) measurements for fish included in the study.

Study component	Cortisol	Sham	Control	Fed	Fasted	F statistic	t ratio	df	p value
Full group caught in June (TL)	326.7±47.8 (69)	331.6±50.1 (69)	325.4±44.0 (69)	—	—	0.33	—	204	0.72
Subset recaptured in August (TL)	337.4±12.9 (19)	336.2±13.8 (16)	322.7±9.0 (23)	—	—	0.58	—	55	0.58
Subset recaptured in October (TL)	307.5±6.5 (5)	339.4±19.1 (13)	331.3±16.4 (10)	—	—	0.67	—	25	0.51
Subset recaptured twice (TL)	298.5 (2)	317.0 (2)	299.7±5.6 (4)	—	—	3.12	—	4	0.15
Laboratory feeding study (TL)	—	—	—	310.0±17.6 (6)	296.7±23.3 (6)	—	0.21	10	0.66
Laboratory feeding study (mass)	—	—	—	381.7±69.8 (6)	373.3±65.6 (6)	—	0.09	10	0.93
Metabolic rate measurements (TL)	330.2±17.9 (6)	—	324.3±17.5 (6)	—	—	—	0.24	10	0.82
Metabolic rate measurements (mass)	494.5±72.7 (6)	—	473.3±72.3 (6)	—	—	—	0.20	10	0.84

Notes: Shown are the TLs cortisol-treated, sham-treated, and control largemouth bass in June; initial TLs of fish recaptured only in August, only in October, and in both August and October; TLs and masses of fish used to obtain fasted and fed biochemical indices; and TLs and masses of fish used for metabolic rate measurements. Within each study, there were no statistical differences among the treatment groups (using analysis of variance, ANOVA; α = 0.05).

of blended trout pellets (Purina Aquamax Grower, Purina Mills Ltd., Missouri) and fresh lake water, using a 50 mL syringe attached to a piece of flexible plastic tubing that placed the food manually in the stomach. Fish in the fasted treatment group were handled in an identical fashion except that no food was injected. Fish were held singly in aerated coolers of fresh lake water for approximately 10 min post-feeding to ensure that no fish regurgitated the mixture. After 7 d (approximately 8 h following the fourth feeding), fish were caught individually from the group tanks and blood samples were withdrawn within 2 min. Plasma was separated and stored as described above. Water temperatures were maintained at 20.0 °C ± 0.9 (mean ± SD) throughout the experiment.

Biochemical analysis

As indicators of recent feeding (Congleton and Wagner 2006), plasma activity of aspartate transaminase and plasma concentrations of cholesterol, glucose, magnesium, total protein, and triglycerides were quantified using a Roche Hitachi 917 analyser (Roche, Basal, Switzerland). All techniques followed the procedural guidelines for standardization and quality assurance established by the Veterinary Laboratory Association Quality Assurance Program and the Canadian Food Inspection Agency External Proficiency Panel, and were carried out by Idexx Laboratories Inc. (Markham, Ontario). For the fish used in the Warner Lake long-term monitoring, pre-treatment (June) plasma samples were not available for all fish recaptured in August and October 2007, and a repeated measures approach was thus not possible. Therefore, if multiple plasma samples (i.e., at multiple capture periods) existed for an individual fish, a subset of plasma samples was analysed such that only a single plasma sample was analysed for each individual. From the June sampling period, 22 samples were analysed as pre-treatment values (n = 8 cortisol-treated, n = 8 sham-treated, n = 6 control). From the August sampling period, samples from 15 cortisol-treated, 15 sham-treated, and 14 control fish were analysed. From the October sampling period, samples from 7 cortisol-treated, 10 sham-treated, and 10 control fish were analysed. All plasma samples from the force-feeding experiment in the laboratory were analysed.

Metabolic effects of cortisol elevation

To determine whether metabolic rate was increased by the short-term elevation of circulating plasma cortisol, 12 largemouth bass were captured by rod-and-reel angling from Lake Opinicon from 21 to 23 June 2008. Fish were transported to the Queen's University Biological Station in aerated coolers, where they were measured (TL), weighed, and size-matched by mass into two groups; cortisol-treated and control (Table 1). Over the 3 d measurement period, four fish were captured per day, and two fish assigned to each treatment group per day. As described above, cortisol-treated fish were injected within 1 h of capture with 10 mg·mL^{-1} cortisol in a coconut oil vehicle at a dose of 0.005 mL·g^{-1}, while control fish were not injected. In this case, we were interested in quantifying a change in metabolic rate as a result of our cortisol treatment, relative to a control animal. Since access to the respirometer was limited, and the objective of this portion of our study was to determine the short-term metabolic consequence of our cortisol treatment rather than to disentangle the specific effect of the cortisol elevation from the handling stress of injecting the implant, sham treatments were not employed for this aspect of the study (see DiBattista et al. 2005 for further rationale). All fish were housed singly in 40 L holding tanks with flow-through lake water for 48–52 h post-capture, both to ensure that metabolic measurements were carried out at peak circulating cortisol concentrations for the cortisol-treated fish (O'Connor et al. 2009), and to ensure that fish were in post-absorptive digestive state (Alsop and Wood 1997).

Metabolic measurements were carried out using the Loligo AutoResp intermittent flow-through respirometry equipment and software (Loligo Systems ApS, Tjele, Denmark) with an 11.4 L chamber (see Gingerich et al. 2009 for full description) from 23–25 June 2008. With this system, dissolved oxygen (DO) levels inside the closed system are measured every second for 15 min. The system is then opened for a 10 min flush period, and metabolic recordings for the next period begin following a 1 min lag after the system is closed. Blank tests were run for 2 to 3 h prior to placing a fish in the respirometry chamber, and oxygen consumption values were corrected accordingly. Fish (two cortisol-treated and two control fish per night) were then placed in the respirometry chamber between 2100 and 2300 hours for a 12 h period. The six lowest recordings were averaged to calculate the SMR for each fish (Steffensen et al. 1994). Mean temperature during the metabolic rate measurements was 23.8 ± 0.6 °C (mean ± SD).

Statistical analysis

For each individual study described above, analysis of variance (ANOVA) models were used to ensure that fish were appropriately size-matched. The χ^2 goodness-of-fit tests were used to test that the fish receiving new PIT tags were evenly distributed across treatment groups for the long-term monitoring aspect of the study.

To analyse mortality patterns of cortisol-implanted versus other treatment groups in the wild, recapture rates (ratios of fish recaptured once, recaptured twice, and never recaptured) were compared among treatment groups using χ^2 goodness-of-fit tests. Given low sample size for ratio estimators, a post-hoc power analysis was conducted to determine the power of this test.

Differences in mean growth rates among the treatment groups over the monitoring period were determined using an analysis of covariance (ANCOVA) with treatment group (cortisol, sham, control) as the independent variable, and initial TL as the covariate. The interaction term was included in the model. Growth rate across the monitoring period was the dependent variables, and was determined for each individual by subtracting the total length upon recapture from the initial total length, and dividing by the number of days between captures. For the fish captured more than once, only the final capture was used to calculate that individual's growth rate. Following a significant ANCOVA, post-hoc Tukey's honestly significant difference (HSD) tests on the treatment effect were used to determine where among the treatment groups the differences lay.

All biochemical parameters in the field were compared among cortisol-treated, sham-treated, and control wild large-

mouth bass in June prior to treatment, in August (54–63 d following treatment) and in October (105–114 d following treatment) using ANOVAs. Tukey's HSD post-hoc tests were employed following significant ANOVAs to determine group differences in mean biochemical parameters. In the complementary laboratory analysis, all plasma biochemical parameters were compared between the fed and fasted fish from the feeding experiment using Student's *t* tests. To ensure that all potentially important biochemical indices were identified, a liberal uncorrected $\alpha = 0.05$ was employed.

To determine whether cortisol treatment resulted in short-term changes in metabolic rate, treatment group were used as the dependent variables in an ANCOVA, with whole-animal SMR as the independent variable, and mass as a covariate. The interaction term was included in the model.

All residuals were tested for normal distribution using goodness-of-fit tests, and for homogeneity of variances using Levene's test, and assumptions were met. All statistical analyses were conducted using JMP 7 (SAS Institute Inc., Cary, North Carolina). All results are reported as mean ± SE, and $\alpha = 0.05$, unless otherwise specified.

Bioenergetics modelling

To explore the relative contribution of increase in SMR to growth rate depression in response to the cortisol injection, a series of simulations of fish growth were conducted using the largemouth bass model developed by Rice et al. (1983) using Fish Bioenergetics software (version 3.0, University of Wisconsin–Madison, Madison, Wisconsin). In a parallel study, field activity rates were found to be similar among the different treatment groups following the cessation of cortisol elevation (O'Connor et al. 2011), and therefore activity was assumed to be equal among treatment groups in all bioenergetic models. We also assumed piscivory (a reasonable assumption for largemouth bass of the sizes used in the present experiment; Heidinger 1975; Keast 1985), and therefore, that food would provide 4000 J of energy·g^{-1} (wet mass). Because the bioenergetics model requires a fish mass variable, mean initial and final masses for control and cortisol-treated fish in the long-term study were estimated using the mass–TL relationship described above. Taking into account the increase in SMR found in our study (see Results), we assumed that SMR remained increased for only the 6 d period of cortisol elevation, and used the bioenergetics model to determine whether an increase in SMR would alone be sufficient to cause the growth depression documented in this study between June and August. This 60 d period was selected rather than the entire 114 d monitoring period so that water temperature could be set as a constant 24 °C in the model.

Population modelling

To explore the potential demographic costs of endocrine stress in terms of individual growth depression, as assessed in the empirical portion of our study, we constructed a deterministic Leslie-matrix population model (Caswell 2001) and compared model runs with and without potential growth depression resulting from cortisol treatment. We also explored the fraction of the population that would need to experience a stress-induced growth depression to see reductions in the population growth rate. Population modelling was conducted as a theoretical experiment and was not indented to provide precise predictions for Warner Lake. The population model was first run with a standard growth model, and then contrasted to a model run in which somatic growth was depressed in fish for a single growing season by the empirical estimate of percentage growth depression measured in the field. We assumed that fish of all age classes (from age 1 to age 10) are influenced by the same percentage of growth depression for the single growing season. The approach followed the work by Edeline et al. (2009).

Largemouth bass length (TL, mm) at age a (years) was modelled using a von Bertalanffy growth model as

$$[1] \quad L_a = L_\infty\{1 - \exp[-0.19(a + 0.024)]\}$$

The default parameter values for the growth model in eq. 1 were taken from the Ontario population of largemouth bass reported in Beamesderfer and North (1995). For simplicity, we assumed no differences in growth among males and females. To account for density-dependence in growth, a negative relationship between population abundance and individual growth estimated for smallmouth bass (Dunlop et al. 2007) was considered as

$$[2] \quad L_\infty = L_{\infty,\max}/(1 + 0.37D^{0.29})$$

where D is the population density (the number of fish of age 1 or older per hectare). The value of $L_{\infty,\max}$ (mm) was determined so that $L_\infty = 560$ mm (an empirical value L_∞ for the Ontario population, Beamesderfer and North 1995) at an intermediate level of population abundance ($D = 3.5$·ha^{-1}). We varied D between 0.5 and 10.0 to check the sensitivity of the model to the population density and found little effect on the outcome. Based on empirical data for maturation of largemouth bass reported by Carlander (1977), the relationship between fish length and proportion of sexually mature female fish at age class a was represented using a sigmoid function as

$$[3] \quad p_a = 1/\{1 - 0.1366\exp[-(L_a - 208.2)]\}$$

We assumed that the sex ratio of the population is 50:50, and the number of recruits was determined by the number of eggs produced by females, since there is no information on density-dependence in spawning stock size-recruitment relationships reported for largemouth bass. To this end, size-dependent fecundity (egg number produced by a female of L_a) $f_{m,a}$ was defined according to Laarman and Schneider (1985) as

$$[4] \quad \log_{10} f_{m,a} = -0.4254 + 3.2857\log_{10} L_a$$

where the subscript m represents mature fish. We assumed there is no sex difference in natural mortality rates but defined size-dependent natural mortality for immature and mature fish separately. Size-dependent annual survival for immature largemouth bass $s_{i,a}$ was based on the study of Gutreuter and Anderson (1985) as

$$[5] \quad s_{i,a} = [1 - 1.2318\exp(-0.01933L_a)]^{12}$$

where the subscript "i" represents immature fish. A fixed annual survival rate (0.73) was assumed for immature fish of 200 mm or larger. Size-dependent annual survival for mature

fish was defined according to Dunlop et al. (2007) reporting in smallmouth bass. We took this relationship based on the finding that mortality rates of largemouth bass and smallmouth bass do not differ significantly (Beamesderfer and North 1995). Based on Dunlop et al. (2007) we defined an upper limit of annual survival rates (0.46) for very large fish based on their description of background mortality as

$$[6] \quad s_{m,a} = \exp(-0.00938L_a + 4.3572)$$

where the subscript "m" represents mature fish. Using the population model defined by eqs. 1–6 we computed the population's finite rate of increase λ as the dominant eigenvalue of the resulting Leslie matrix M (Caswell 2001). The form of the Leslie matrix we used was

$$[7] \quad M = \begin{pmatrix} s_0 f_1 & s_1 f_2 & \cdots & s_{a_{max}-2} f_{a_{max}-1} & s_{a_{max}-1} f_{a_{max}} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & & 0 & 0 \\ \vdots & & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{a_{max}-2} & 0 \end{pmatrix}$$

The age-specific survival and fecundity (egg number per female at age a) in the matrix was represented as

$$[8] \quad s_a = p_m S_{m,a} + (1 - p_m) S_{i,a}$$

and

$$[9] \quad f_a = p_m f_{m,a}$$

The survival from eggs to age-1 fish, s_0, was determined by the method of Vaughan and Saila (1976), on the assumption that the population is at equilibrium without individual growth depression. We assumed $a_{max} = 11$, and sensitivity analyses showed that increasing a_{max} caused negligible changes in the population growth rate λ.

Results

Standardization among treatment groups

There were no differences in initial TLs among the three treatment groups from Warner Lake in June (Table 1). There were also no differences in initial TLs detected among the subsets of each treatment group recaptured only in August, only in October, or at both sampling periods (Table 1). There were no differences among the treatment groups in the proportion of fish given new PIT tags relative to fish already carrying PIT tags ($\lambda^2 = 2.53$, df = 2, $p = 0.28$). Similarly, there were no differences in mass or TL between the force-fed and fasted treatment groups in the complementary laboratory study examining biochemical indices of fasting (Table 1), and there were also no differences in mass or TL between the cortisol-treated and control fish used for metabolic rate measurements (Table 1).

Long-term effects of transient plasma cortisol elevation in wild largemouth bass

In total, 86 fish were recaptured once: 24 cortisol-treated fish, 29 sham-treated fish, and 33 control fish. Of these, 58 were recaptured once in August: 19 cortisol-treated, 16 sham-treated, and 23 control fish. Twenty-eight were recaptured once in October: 5 cortisol-treated, 13 sham-treated, and 10 control fish. An additional 8 fish were recaptured at both sampling periods: 2 cortisol-treated, 2 sham-treated, and 4 control fish (Table 2). While fewer cortisol-treated fish over the study period were recaptured than control and sham-treated fish, the ratios of fish recaptured once, recaptured twice, or never recaptured did not differ among the three groups ($\lambda^2 = 3.77$, df = 4, $p = 0.44$). This result indicates mortality rates did not differ significantly among the groups during the summer months. However, a power analysis revealed that with only 24 fish per treatment group recaptured across the monitoring period (the minimum number of fish per treatment group recaptured once in our study), the power of our study to detect biologically relevant levels of mortality (relative to the control group) was low (Table 3).

Mean growth rate (mean increase in TL per day for each fish) over the monitoring period was significantly lower for the cortisol-treated fish than for the control and sham-treated fish (model $F_{[3,84]} = 9.69$, $p < 0.001$; treatment group $F_{[2,2]} = 9.94$, $p < 0.001$; Fig. 1). As expected, initial TL was also important in predicting growth over the season (initial TL $F_{[1,1]} = 26.89$, $p < 0.001$). The interaction effect was not significant (interaction $F_{[2,2]} = 0.01$, $p = 0.98$). The mean growth rate for control fish was 0.15 ± 0.02 mm·d^{-1} (mean ± SE), while the growth rate for the sham-treated fish was 0.09 ± 0.06 mm·d^{-1}, and the mean growth rate for the cortisol-treated fish was 0.01 ± 0.02 mm·d^{-1}, which amounts to a 93% decrease in growth rate for the cortisol-treated group relative to the control group, and an 89% decrease in growth rate relative to the sham-control group. Note that for fish recaptured twice, only the data from October was used in the statistical analysis.

Biochemical indices of fasting

Among fish included in the long-term study from Warner Lake, no differences in biochemical variables were detected among the treatment groups in June, prior to treatment (Table 4). Chloride varied significantly among the treatment groups in August (54–63 d following treatment), with sham-treated fish exhibiting significantly higher plasma chloride concentrations than cortisol-treated fish (Table 5). Similarly, sham-treated bass exhibited significantly higher plasma glucose concentrations than cortisol-treated bass in October (105 to 114 d following treatment; Table 6). No other differences among treatment groups were detected (Tables 5 and 6).

Individuals that were force-fed exhibited significantly lower plasma sodium concentrations than bass that were fasted for 7 d, and significantly higher plasma concentrations of triglycerides (Table 7). No other differences were detected between fed and fasted fish in the laboratory (Table 7).

Short-term metabolic effects of cortisol elevation

Both cortisol treatment and mass significantly impacted mean SMR measured ~56 h after treatment with cortisol (model $F_{[3,8]} = 46.07$, $p < 0.01$; Fig. 2). Mass was the main effect (mass $F_{[1,1]} = 98.67$, $p < 0.01$), but treatment group was also a significant effect (treatment $F_{[1,1]} = 20.20$, $p < 0.01$), as was the interaction of these two factors (interaction $F_{[1,1]} = 12.54$, $p < 0.01$). Mean mass-corrected SMR for

Table 2. Number of fish recaptured once, twice, or never recaptured in the cortisol-treated, sham-treated, and control groups of fish.

Recaptured subset	Cortisol	Sham	Control
Fish recaptured once	24	29	33
Fish recaptured twice	2	2	4
Fish never recaptured	43	38	32

Note: There were 69 fish treated in each group in June. There are no differences among the treatment groups in the ratios of fish captured once, fish recaptured twice, and fish never recaptured among treatment groups (χ^2 tests; $\lambda^2 = 3.77$, df = 4, $p = 0.44$).

Table 3. Results of a post-hoc power analysis to determine the power of detecting a decline in recapture rate in the sham-treated or cortisol-treated group relative to the control group, using a conservative estimate of 24 fish recaptured once per treatment group across the monitoring period.

Theoretical % mortality (relative to the control group)	Power ($1 - \beta$)
5	0.05
10	0.10
20	0.18
30	0.46
50	0.86
90	0.99

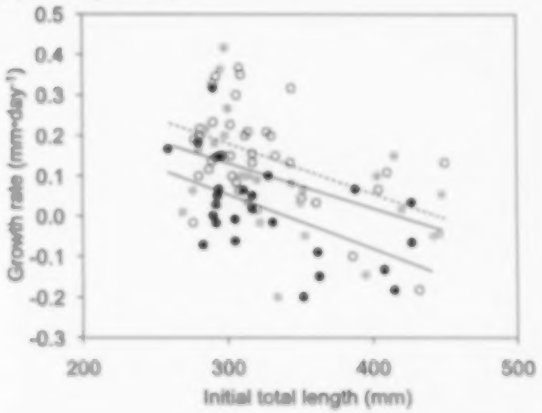
Note: Power analysis reveals that biologically relevant declines would be difficult to detect given the small sample size.

control fish was 79 ± 2 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$, compared with 93 ± 2 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for cortisol-treated fish; this represented an 18% increase in SMR, on average, as a result of cortisol elevation.

Bioenergetics modelling

During the 60 d growth period between June and August, at a mean water temperature of 24 °C, the control fish grew from an initial mean mass of 459.1 g (calculated using the mass–TL relationship from the TL of 320.1 mm) to a mean final mass of 497.7 g (calculated from the TL of 329.2 mm). To achieve this level of growth, it was estimated in the bioenergetics model that individuals would have to have consumed on average 373.6 g of fish prey, with 33% of consumed food allocated to growth. Applying the same growth and consumption rates over the same period to the cortisol-treated fish revealed that these fish (with an initial mean mass of 529.2 g calculated from the TL of 333.5 mm) would have needed to consume on average 410.9 g of prey. Assuming piscivory, food would provide 4000 $J \cdot g^{-1}$. Taking into account the increase in SMR, and assuming that SMR remained increased for only the 6 d period of cortisol elevation, the model predicted that the cortisol-treated fish should have achieved a final mass of 568.7 g. From our growth data, we calculated from the mass–TL relationship that the control fish achieved a final mass of only 530.9 g (from the TL of 334.3 mm). Thus, the bioenergetics modelling revealed that either the metabolic rate of the cortisol-treated fish must have remained elevated beyond the 6 d period of cortisol elevation, or there must have been an additional mechanism causing the growth depression, such as a reduction in foraging, or sustained metabolic costs as a result of the transient stressor.

Fig. 1. Growth rate (change in total length (TL) in mm per day) plotted as a function of initial TL for cortisol-treated ($n = 26$), sham-treated ($n = 31$), and control ($n = 37$) largemouth bass. Cortisol-treated fish are represented by black-filled circles, sham-treated fish are represented by the grey-filled circles, and control fish are represented by the open circles. The mean growth rate for the cortisol-treated fish was lower than the mean growth rate for the sham-treated and control fish (Tukey's honestly significant difference (HSD) post-hoc test following a significant analysis of covariance (ANCOVA); model $F_{[5,84]} = 9.69$, $p < 0.001$; treatment group $F_{[2,2]} = 9.94$, $p < 0.001$). As expected, initial TL was also important in predicting growth over the season (initial TL $F_{[1,1]} = 26.89$, $p < 0.001$), but as there were no differences in the mean TL among the treatment groups at the onset of the experiment, this does not account for the documented difference in growth rates among the groups. The interaction term was not significant (interaction $F_{[2,2]} = 0.01$, $p = 0.98$).



The potential population-level consequences of stress-induced growth depression

Decreased somatic growth resulting from short-term cortisol implants affects age-specific survival and age-specific fecundity, which is predicted to result in a decrease in population growth rate λ of a prototypical largemouth bass population (Fig. 3*a*). For example, in our model, a 50% decline in somatic growth rate of all individuals of the population in a single growing season is predicted to result in a 14% decrease in population growth rate, while a 99% decline in somatic growth rate is predicted to result in a 37% decrease in population growth rate. In the present experiment, cortisol-treated fish showed an 89% depression in growth rate over the growing season compared with sham-treated fish (Fig. 1). When all the fish of the population would experience a similar level of stress, the decline of population growth rate as a result of such growth depression over a single growing season would be 23%. Since most stressors do not affect all individuals equally, we also modelled the percentage of the population that would need to experience growth depression to see biologically interesting reductions in population growth rate. We found that to experience a 5% and 10% reduction in population growth, 19% and 39% of the largemouth bass population, respectively, would need to experience stress causing the growth depression documented in the empirical component of this study (Fig. 3*b*).

Table 4. Plasma biochemistry (mean ± SE) of cortisol-treated (n = 8), sham-treated (n = 8), and control (n = 6) wild largemouth bass prior to treatment in June.

Parameter	Control	Sham	Cortisol	F statistic	Error df	p value
Aspartate transaminase ($U \cdot L^{-1}$)	40±12.2	46±10.6	38±10.6	0.14	19	0.87
Ca^{2+} ($mmol \cdot L^{-1}$)	3.4±0.08	3.5±0.07	3.5±0.07	0.67	19	0.52
Cl^- ($mmol \cdot L^{-1}$)	112±3.3	123±2.9	119±2.9	3.08	19	0.07
Cholesterol ($mmol \cdot L^{-1}$)	15±1.8	13±1.6	17±1.6	1.57	19	0.23
Glucose ($mmol \cdot L^{-1}$)	2.5±0.10	2.6±0.09	2.4±0.09	1.25	19	0.31
Mg^{2+} ($mmol \cdot L^{-1}$)	1.2±0.05	1.3±0.04	1.2±1.04	1.79	19	0.19
P^{5-} ($mmol \cdot L^{-1}$)	2.4±0.19	2.6±0.16	2.4±0.16	0.41	19	0.67
K^+ ($mmol \cdot L^{-1}$)	3.0±0.3	3.4±0.2	3.5±0.2	0.82	19	0.45
Na^+ ($mmol \cdot L^{-1}$)	167±3.8	178±3.3	174±3.3	2.45	19	0.11
Total protein ($g \cdot L^{-1}$)	40±2.0	42±1.7	42±1.7	0.24	19	0.79
Triglycerides ($mmol \cdot L^{-1}$)	3.9±0.63	2.8±0.55	2.6±0.55	1.22	19	0.32

Note: There are no statistical differences in plasma biochemistry among the groups (one-way analysis of variance, ANOVA; α = 0.05).

Table 5. Plasma biochemistry (mean ± SE) of cortisol-treated (n = 15), sham-treated (n = 15), and control (n = 14) wild largemouth bass 54–63 d after treatment, in August.

Parameter	Control	Sham	Cortisol	F-statistic	Error df	p value
Aspartate transaminase ($U \cdot L^{-1}$)	37±6.4	56±6.4	37±6.7	2.97	41	0.06
Ca^{2+} ($mmol \cdot L^{-1}$)	3.2±0.06	3.3±0.06	3.3±0.06	0.36	41	0.70
Cl^- ($mmol \cdot L^{-1}$)	**114±2.9$_{ab}$**	**120±2.9$_a$**	**109±3.0$_b$**	**3.57**	**41**	**0.04**
Cholesterol ($mmol \cdot L^{-1}$)	12±0.8	12±0.8	12±0.8	0.02	41	0.98
Glucose ($mmol \cdot L^{-1}$)	2.4±0.12	2.7±0.12	2.6±0.12	1.67	41	0.20
Mg^{2+} ($mmol \cdot L^{-1}$)	2.3±0.11	2.5±0.11	2.4±0.11	0.63	41	0.54
P^{5-} ($mmol \cdot L^{-1}$)	2.3±0.11	2.5±0.11	2.4±0.11	0.63	41	0.54
K^+ ($mmol \cdot L^{-1}$)	2.6±0.31	2.6±0.31	2.4±0.32	0.10	41	0.90
Na^+ ($mmol \cdot L^{-1}$)	166±1.8	170±1.8	167±1.9	1.41	41	0.26
Total protein ($g \cdot L^{-1}$)	39±1.0	39±1.0	41±1.1	1.96	41	0.15
Triglycerides ($mmol \cdot L^{-1}$)	2.7±0.40	1.9±0.40	1.9±0.42	1.19	41	0.31

Note: Bold text indicates variables for which statistically significant differences were detected; treatment groups that differed are indicated with different letters (one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) post-hoc tests; α = 0.05).

Table 6. Plasma biochemistry (mean ± SE) of cortisol-treated (n = 7), sham-treated (n = 10), and control (n = 10) wild largemouth bass 104–115 d after treatment (October).

Parameter	Control	Sham	Cortisol	F-statistic	Error df	p value
Aspartate transaminase ($U \cdot L^{-1}$)	30±11.9	57±11.9	40±14.2	1.26	24	0.30
Ca^{2+} ($mmol \cdot L^{-1}$)	3.5±0.12	3.6±0.12	3.3±0.14	1.51	24	0.24
Cl^- ($mmol \cdot L^{-1}$)	114±4.7	100±4.7	125±5.7	3.04	24	0.07
Cholesterol ($mmol \cdot L^{-1}$)	13±1.4	14±1.4	12±1.7	0.67	24	0.52
Glucose ($mmol \cdot L^{-1}$)	**2.2±0.19$_{ab}$**	**2.8±0.19$_a$**	**2.0±0.23$_b$**	**4.55**	**24**	**0.02**
Mg^{2+} ($mmol \cdot L^{-1}$)	1.4±0.05	1.4±0.05	1.3±0.06	0.24	24	0.79
P^{5-} ($mmol \cdot L^{-1}$)	2.4±0.12	2.3±0.12	2.4±0.14	0.09	24	0.91
K^+ ($mmol \cdot L^{-1}$)	2.1±0.37	2.0±0.37	2.6±0.45	0.66	24	0.52
Na^+ ($mmol \cdot L^{-1}$)	173±1.9	170±1.9	171±2.3	0.56	24	0.58
Total protein ($g \cdot L^{-1}$)	39±1.4	40±1.4	38±1.7	0.66	24	0.53
Triglycerides ($mmol \cdot L^{-1}$)	2.5±0.71	2.1±0.71	3.6±0.84	1.00	24	0.38

Note: Bold text indicates variables for which statistically significant differences were detected; treatment groups that differed are indicated with different letters (one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) post-hoc tests; α = 0.05).

Discussion

We found that a short-term cortisol implant resulted in changes in the long-term growth rate of wild largemouth bass in a natural lake. In the field, we found few long-term changes in plasma biochemistry, and no changes in plasma biochemistry that were consistent with complete fasting, as indicated by the complementary laboratory study. In exploring other potential mechanisms of the stress-induced growth rate depression, we found in the laboratory that metabolic rate was elevated during the period of cortisol elevation. However, bioenergetics modelling suggested that this increased metabolic rate was not sufficient to explain the observed growth depression in the field if metabolic rate

Table 7. Plasma biochemistry (mean ± SE) of fed and fasted wild largemouth bass in the laboratory.

Parameter	Fed	Fasted	*t* ratio	df	*p* value
Aspartate transaminase ($U \cdot L^{-1}$)	37±19	57±19	0.73	8	0.48
Ca^{2+} ($mmol \cdot L^{-1}$)	3.2±0.1	3.2±0.1	0.09	8	0.92
Cl^{-} ($mmol \cdot L^{-1}$)	75±5	88±5	1.89	8	0.09
Cholesterol ($mmol \cdot L^{-1}$)	12±1	15±1	1.74	8	0.11
Glucose ($mmol \cdot L^{-1}$)	9.9±1.0	6.8±1.0	–2.13	8	0.06
Mg^{2+} ($mmol \cdot L^{-1}$)	1.3±0.0	1.3±0.0	–0.66	8	0.53
P^{5-} ($mmol \cdot L^{-1}$)	1.6±0.1	1.9±0.1	1.79	8	0.11
K^{+} ($mmol \cdot L^{-1}$)	2.8±0.3	3.2±0.3	0.85	8	0.42
Na^{+} ($mmol \cdot L^{-1}$)	**145±2**	**153±2**	**2.86**	**8**	**0.02**
Total protein ($g \cdot L^{-1}$)	49±2	47±2	–0.77	8	0.46
Triglycerides ($mmol \cdot L^{-1}$)	**2.6±0.4**	**0.6±0.4**	**–3.59**	**8**	**<0.01**

Note: Bold text indicates statistical differences using Student's *t* tests ($\alpha = 0.05$).

Fig. 2. Whole-animal standard metabolic rates depicted as a function of mass and treatment group (control and cortisol-treated fish; $n = 6$ in each group). Cortisol-treated fish are represented by filled circles, while control fish are represented by open circles. Mass, treatment group, and the interaction effect were all significant (model $F_{[3,8]} = 46.07$, $p < 0.001$; mass $F_{[1,1]} = 98.67$, $p < 0.001$; treatment $F_{[1,1]} = 20.20$, $p < 0.01$; interaction $F_{[1,1]} = 12.54$, $p < 0.01$; $\alpha = 0.05$).

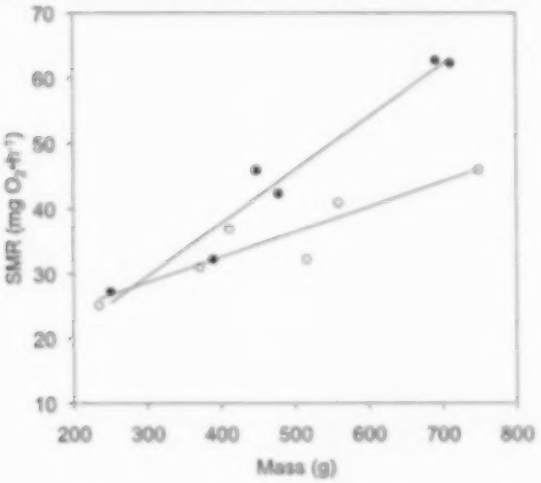
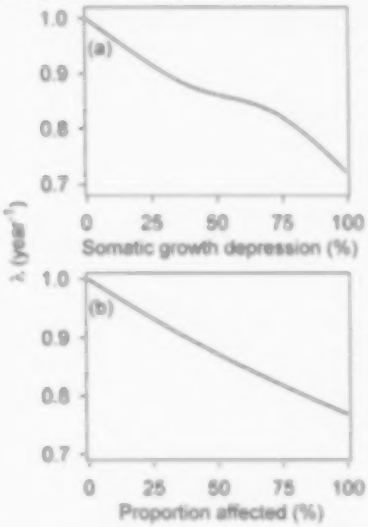


Fig. 3. The demographic cost of endocrine stress estimated by Leslie matrix projection modelling. (*a*) Estimated population rates of increase (λ) plotted against hypothetical somatic growth depression, with all individuals of the population being assumed to experience the same level of growth depression. (*b*) Estimated population rates of increase (λ) plotted against the proportion of population experiencing an 89% somatic growth depression for a single growing season, which corresponds to the empirical estimate.



elevation is maintained only while circulating cortisol is elevated. Therefore, growth depression is likely to be explained by other mechanisms such as energy loss resulting from coping with the stressor (i.e., metabolic costs are sustained beyond the elevation of plasma cortisol), or a reduction in foraging that was not captured using our measured biochemical indices. While we found no differences in recapture rates among the various treatment groups, suggesting no differences among groups in mortality across the summer, the power of our study was low, and results were thus inconclusive. However, even without differences in mortality rate among the groups, growth depression resulting from short-term stress was found to potentially alter long-term population growth rate as indicated by a complementary theoretical population modelling exercise. For a reduction in population growth rate to occur, a substantial fraction of the largemouth bass population would need to experience a stress event causing individual growth depression.

Mechanisms of long-term growth suppression

The results of our study demonstrate that a cortisol hormone implant constitutes a challenge from which fish are unable to fully recover during a single growing season. We also found that the elevation of circulating cortisol was associated with an increase in SMR. This result was consistent with previous studies on laboratory rainbow trout (*Oncorhynchus mykiss*), where elevations of plasma cortisol have been associated with an increase in SMR (Morgan and Iwama 1996). Furthermore, this is consistent with previous studies examining chronic stressors, where both social stress in rainbow trout (Sloman et al. 2000) and chronic stress in green sturgeon (*Acipenser medirostris*) have been shown to increase SMR (Lankford et al. 2005), and is consistent with the prevalent notion that elevated cortisol in fish is associated with an

increase in catabolic activity and energy use (De Boeck et al. 2001). However, our bioenergetics modelling suggested that a short-term increase in SMR (i.e., an increase during only the 6 d period of cortisol elevation) would not be sufficient to account for the observed long-term differences in growth rate among treatments without some concurrent additional mechanism such as a reduction in feeding.

Stress in largemouth bass reduces feed intake (Siepker et al. 2006), and administration of exogenous cortisol hormone implants has also been shown to reduce appetite in rainbow trout (Gregory and Wood 1999). We did look at fasting and its biochemical correlates, but the most noteworthy finding was that there were very few changes either between the fed and fasted fish in the laboratory or among the cortisol-treated, sham-treated, and control fish over the 114 d monitoring period in the wild. These data suggested that wild fish defend physiological homeostasis in the measured plasma parameters despite fasting. However, stability of biochemical profiles does not exclude the possibility that feed intake of cortisol-treated fish was reduced relative to control fish, potentially explaining the growth depression observed in the field. Further studies that incorporate different response metrics of body condition and feeding history, and more detailed behavioural studies are necessary to understand the potential long-term changes in foraging behaviour as a result of elevated circulating plasma cortisol in largemouth bass and other fish in the wild.

The combination of results from the present study revealed that transient elevations of cortisol carry both immediate energetic costs and long-term growth costs. In addition to the possibilities investigated in the present study of cortisol-induced changes in feeding behaviour and metabolic rate, other factors may have contributed to the long-term impairment of growth by transient cortisol elevation. Both stress and experimental elevations of plasma cortisol are associated with reductions in immune function and increases in disease susceptibility (Wendelaar-Bonga 1997; Barton 2002; Greenberg et al. 2002), and it is possible that compensating for the long-term challenges associated with disease constitutes a persistent energetic cost that could also help to explain the differences in growth detected among the treatment groups in our study. Stress and experimental elevations of plasma cortisol are also associated with complex behavioural changes, including changes in social dominance (Barton 2002; Greenberg et al. 2002). Previous research looking at behavioural metrics found rapid resubmission of normal behavioural patterns after a single stress event in wild fish (e.g., resumption of normal behaviour in northern pike, *Esox lucius*, following a catch-and-release angling event; Klefoth et al. 2008; Arlinghaus et al. 2009). Similarly, previous research in Warner Lake indicates that largemouth bass treated with cortisol have similar activity levels when compared with sham-treated and control fish (O'Connor et al. 2010). However, cortisol-treated fish in the current study may have been altering their behaving on a fine scale in a way that also increased their energetic expenditure beyond the cessation of the cortisol hormone implant. Further research that examines the long-term metabolic costs of short-term cortisol elevation is necessary to fully understand the energetic costs of a short-term stressor in wild, free-swimming animals. Particularly useful would be research that incorporates detailed behavioural data to more thoroughly explore the feeding behaviour and activity rates of fish that have been exposed to a transient stressor or to transient cortisol elevation.

Potential consequences of individual physiological stress for the population

The results of the present study did not provide any evidence of differing mortality rates among the treatment groups. However, the power to detect biologically meaningful differences in mortality rates among the groups was low. Yet the long-term energetic costs, particularly the persistent growth costs, might have implications for the long-term survival and reproductive output of fish, and even population growth rates, without an immediate increase in mortality. Mortality rates in this species are size dependent, and female fecundity and female preferences scales with male size (Dunlop et al. 2007). Our population modelling was used to explore potential scenarios of how individual growth depression might affect population growth rate, and suggested that somatic growth depression caused by endocrine stress could result in a substantial decrease in population growth. This theoretical modelling exercise suggests that the experience of sublethal stress in wild fish has the potential to reduce long-term survival and lifetime reproductive out, and affect population growth rate, as has been shown in laboratory populations (Edeline et al. 2009). It is important to note that our population model indicated that a substantial fraction (39%) of the population would need to be exposed to a single stress event to cause a 10% reduction in population growth rate. Such wide-scale stress could conceivably occur as a result of environmental challenges such as oxygen depletion, or anthropogenic activities such as intense boating activity, or catch-and-release angling. It is important to also consider that in the model, growth was assumed to return to normal pre-stress levels after the single season of growth suppression. In reality, compensatory growth might occur (see Ali et al. 2003), and future studies monitoring fish over a longer period of time would be useful in determining when and to what degree this occurs.

Study limitations

The cortisol administered in our study generated supraphysiological concentrations of circulating cortisol (~2000 ng·mL^{-1}) as reported elsewhere in detail (O'Connor et al. 2009). In the current study, the field setting precluded analysis of pilot samples prior to initiating the full experiment. The result was that the dose selected, based on literature for salmonid fish (Gamperl et al. 1994), elicited plasma cortisol concentrations in largemouth bass that were an order of magnitude higher than endogenous levels during a challenge (~300 ng·mL^{-1}). However, despite the pharmacological dose, the increase in SMR with cortisol treatment was comparable in magnitude with previous studies where chronic stressors initiated the physiological response (Sloman et al. 2000; Lankford et al. 2005). Following a cortisol injection of the same dose in another study, largemouth bass exhibited a typical glucose response to elevated plasma cortisol (O'Connor et al. 2009), and no immediate mortality was observed in cortisol-treated fish (O'Connor et al. 2009, 2011). While acknowledging the methodological limitation of a supraphysiological dose, our examination of the long-term effects of cortisol elevation in

a wild free-swimming fish provides unique insight into the physiological mechanisms that drive whole-animal consequences of stress. The current study provides a first step in elucidating the nature of long-term consequences of stress in a wild fish population, and may inspire future research aimed at understanding the magnitude of effect caused by a single stressor of interest.

We used total length (TL) as a measure of fish size, and the increases in TL per day over the monitoring period were used as a measure of fish growth. The use of TL as a single measurement of growth is limited, because it does not take into account any measure of body condition (i.e., relative mass or girth per TL), which can also be affected by cortisol treatment (e.g., Barton et al. 1987). Furthermore, in our study there was no specific assessment of measurement error associated with taking measurements of total length (i.e., measuring the same fish multiple times during a single sampling period), or with other sources of variation (e.g., males versus females, or single versus double recapture). Given that decreases in TL were documented across the monitoring period in some individuals, it is clear that there was a level of error associated with taking TL measurements. However, we have no reason to suppose that sources of measurement error differentially affected a specific treatment group, and therefore we are confident that the differences among treatment groups reflect true differences, and not an anomaly caused by measurement error. Nonetheless, future studies should certainly include measurements of both TL and body mass and condition, as well as assessments of measurement error. Measurements of body condition would also yield more detailed insight into the potential for compensatory growth in a cortisol-treated fish (Ali et al. 2003).

A final limitation of our study relates to the population modelling exercise. Although our model illustrated the potential population-level effects of a single stress event affecting a portion of the target population, there are limitations to this model. We only used one process of density-dependence (i.e., density-dependence in growth), and we did not include density-dependent fecundity and mortality in the model because no data was available for largemouth bass. We also did not explicitly include size-dependent mate choice of males by females, because again, the data was not available for this species. Our model nevertheless served as a test of the impact of growth depression by holding the general population model constant and varying only the growth submodel. Thus, our predictions of population level effects of growth depression should hold qualitatively, although we cannot claim precise predictive power. Another limitation arises from modelling a single fish population closed to immigration, emigration, and fishing, and ignoring interspecies interactions. Interspecific interactions might accelerate or suppress the magnitude of the reduction of population growth rate in the target population. Finally, as the experimental data provided no information about the difference in growth depression between males and females, we assumed that both males and females experienced the same level of growth rate depression. The reduction of population growth rate shown in the present study essentially resulted from a reduction of lifetime reproductive success in females through decreased fecundity and increased mortality due to individual growth depression. Male largemouth bass provide nest-guarding parental care, and if the quality of the care depends on males' size (see Hanson and Cooke 2009), the reduction in male size might result in a further reduction of population growth rate.

To conclude, despite the limitations mentioned above, our study is the first to show growth rate depression after a single stress event in a wild free-swimming fish. Bioenergetics modelling suggests that mechanisms such as long-term metabolic costs or reduced feeding would account for this growth rate depression. Simple population modelling exercises suggest that if a substantial proportion of the population experiences such a stress event, the population-level growth rate will be affected. Across a range of taxa, there have been few studies that have studied or documented instances in which stress at the level of the individual cascades to influence population-level processes (Calow and Forbes 1998). Understanding the relationships between sublethal stressors and ecologically relevant measures such as individual or even population-level growth rates is critical to further understand the "ecology of stress" in wild fish, particularly given the level of environmental change and disturbance occurring in aquatic ecosystems.

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Energetic costs and benefits of cyclic habitat switching: a bioenergetics model analysis of diel vertical migration in coregonids

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Abstract: Recent studies on diel vertical migration (DVM) of two coregonid species (*Coregonus* spp.) in Lake Stechlin (Germany) have suggested that the nocturnal distribution of fish is linked with metabolic benefits. We used a spatially explicit bioenergetics-based foraging model to test whether energetic constraints contribute to explain DVM of both species. The newly parameterized model was compared with independent data from Lake Stechlin that covered a 9 month period. Predicted growth rates matched observed growth rates of each fish species reasonably well. The simulation of different migration scenarios showed that even slight changes in night-time depths modified growth rates, primarily owing to temperature-dependent respiration. Fish that performed DVM grew faster than nonmigratory fish that occupied deep hypolimnetic water over a diel cycle. However, the most energy-efficient strategy simulated had fish remaining within the metalimnion. Here, energetic benefits (foraging) clearly outweighed higher energetic costs (respiration) in the warmer waters. Although DVM can be energetically beneficial, it is not the most efficient strategy performed by coregonids in Lake Stechlin. We suggest that multiple factors, rather than bioenergetics efficiency alone, are the evolutionary basis for DVM of many freshwater fish species.

Résumé : Des études récentes sur la migration verticale journalière (DVM) de deux espèces de corégonidés (*Coregonus* spp.) dans le lac de Stechlin (Allemagne) indiquent que la répartition des poissons la nuit s'explique par des bénéfices métaboliques. Un modèle de recherche de nourriture basé sur la bioénergétique et spatialement explicite nous permet de vérifier si les contraintes énergétiques expliquent la DVM chez les deux espèces. Le modèle nouvellement paramétré a été comparé à des données indépendantes prélevées au lac de Stechlin sur une période de neuf mois. Les taux de croissance prédits correspondent raisonnablement bien aux taux de croissance observés chez chaque espèce de poisson. La simulation de divers scénarios de migration montre que même de faibles changements dans les profondeurs utilisées la nuit modifient les taux de croissance surtout à cause de la respiration qui est dépendante de la température. Les poissons qui font une DMV croissent plus rapidement que les poissons non migrateurs qui restent dans les eaux hypolimnétiques profondes durant le cycle journalier. Cependant la stratégie la plus efficace énergétiquement dans les simulations est celle dans laquelle les poissons demeurent dans le métalimnion. À ces profondeurs, les bénéfices énergétiques (alimentation) surpassent nettement les coûts énergétiques accrus (respiration) dans les eaux plus chaudes. Bien que la DVM puisse être avantageuse du point de vue énergétique, ce n'est pas la stratégie la plus efficace que les corégones utilisent dans le lac de Stechlin. Nous croyons que c'est une multitude de facteurs plutôt que la seule efficacité énergétique qui est la base évolutive de la DVM chez plusieurs espèces de poissons d'eau douce.

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Introduction

Diel vertical migration (DVM) is a behavioral strategy commonly observed in many aquatic organisms (Brett 1971*a*; Lampert 1989; Gjelland et al. 2009). The usual DVM pattern is to stay in the deeper parts of the lake during the day, ascend into shallower layers at dusk, reside there during the night, and descend back to deeper layers at dawn. This regular DVM is often observed in coldwater fish populations living in deep, stratified lakes (Janssen and Brandt 1980; Hrabik et al. 2006). Change in illumination strength over the diel cycle is a reliable trigger for the onset of upward and downward migrations (Levy 1990*a*; Gjelland et al. 2009).

There are three primary hypotheses regarding the evolutionary basis for DVM, namely, predator avoidance, feeding opportunity, and bioenergetics efficiency. However, predator avoidance is usually considered to be the main driver of DVM in fish (Hrabik et al. 2006). Most piscivores require some light to feed, therefore prey spatially co-occur with their predators only during the safety of darkness. However, because planktivores are also visual feeders, an illumination window exists in which feeding of planktivores is still possi-

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ble, but piscivore feeding is largely impaired. This particular period is called the antipredation window (Clark and Levy 1988; Scheuerell and Schindler 2003). Predator avoidance is closely coupled with feeding opportunity, because zooplankton density usually declines with water depth such that the highest prey availability in lakes can be found close to and sometimes above the thermocline (Mehner et al. 2005). A third hypothesis regarding DVM is referred to as bioenergetics efficiency, and is proposed for situations where water layers that minimize maintenance costs and maximize feeding efficiency are spatially decoupled (Bevelhimer and Adams 1993; Sims et al. 2006). Under this hypothesis, regular switching between the layers by DVM may be energetically most efficient.

These three evolutionary explanations of DVM are not mutually exclusive, and in most cases a single hypothesis does not explain the variability of all observed migration patterns (Levy 1990*b*; Hardiman et al. 2004). Understanding the mechanisms responsible for DVM in fish is particularly challenging because experimentation at appropriate spatial scales with migration amplitudes of 10 to >70 m is almost impossible. Alternatively, modeling can assist empirical field work and laboratory experiments in studying spatially and temporally variable distribution patterns of aquatic animals along vertical gradients. Accordingly, DVM has been modeled for shrimps (*Mysis diluviana*, Boscarino et al. 2007), daphnids (*Daphnia* spp., Rinke and Petzoldt 2008), and fishes (Bevelhimer and Adams 1993; Tolonen 1999; Jensen et al. 2006).

Modeling is particularly useful for systems in which empirical data suggest interactive or even contradictory evolutionary causation of DVM. A good example is Lake Stechlin, a deep lake in northeastern Germany, in which two planktivorous coregonid species, the common European vendace (*Coregonus albula*) and the endemic Fontane cisco (*Coregonus fontanae*), coexist (Helland et al. 2008). Both species perform DVM, but with seasonally varying amplitudes related to the vertical temperature gradient and stratification in the lake (Helland et al. 2007; Mehner et al. 2007; Busch and Mehner 2009). While predation avoidance is considered of low importance owing to the extremely low density of pelagic piscivores, the strong correlation between night-time population depth and temperature suggests that bioenergetics advantages contribute to the causation of DVM (Mehner et al. 2007, 2010). However, the bioenergetics efficiency of vertically migrating fish along temperature gradients is intrinsically linked with the potential feeding rates in the habitats. Foraging is modified by prey density, prey composition and size, illumination strength, and temperature (Werner and Hall 1974; Persson 1986; Vogel and Beauchamp 1999). Therefore, a spatially explicit bioenergetics model applied to vertically migrating fish may elucidate whether the empirically observed diel distribution patterns of the coexisting coregonids reflect a bioenergetically optimum strategy.

To better understand the interplay between feeding opportunity and the energetic benefits and costs during DVM, we reparameterized a bioenergetics model (Stockwell and Johnson 1997, 1999) to describe the coexisting coregonids of Lake Stechlin, and compared the model results with our detailed empirical observations. This new approach provides four major advantages over already existing models for coregonids (Helminen et al. 1990; Rudstam et al. 1994; Tolonen 1999). First, the model estimates the consumption rate of fish as a function of prey density and light intensity by incorporating a light-dependent functional response for vendace and cisco (Ohlberger et al. 2008*a*). Second, this model applies temperature-sensitive physiological parameters (consumption and respiration) that have been experimentally determined for both species to reduce the number of parameters borrowed from other species (Ney 1993). Third, the model is run in a spatially explicit way at high temporal resolution, thus mimicking the changing biotic and abiotic environment the fish experience during their daily migrations. Finally, the long-term empirical observations on coregonid DVM in Lake Stechlin facilitate a validation of model results, because observed and predicted growth rates can be directly compared.

Based on previous studies showing little evidence for predation risk as the main driver of DVM (Mehner et al. 2007), we hypothesized that bioenergetics contributed decisively to explaining the evolutionary benefits of coregonid DVM in Lake Stechlin. We tested this hypothesis by comparing feeding rates and the respiration costs of differing migration strategies. In a first step, the model was run to mimic the empirically observed migration amplitudes, and validated with empirical growth data. In a second step, two simulations were compared that slightly modified the night-time depths and hence the migration amplitudes of fish. Finally, we simulated scenarios with no migration at all.

Materials and methods

Model

We applied a bioenergetics-based foraging model originally established for kokanee salmon (*Oncorhynchus nerka*) (Bevelhimer and Adams 1993; Stockwell and Johnson 1997, 1999), but parameterized it to describe the coregonids of Lake Stechlin. The model used a balanced energetics equation (Kitchell et al. 1977) in which consumed energy (C) was allocated to metabolism (R), egestion (F), excretion (U), and growth (G):

$$C = R + F + U + G \quad (1)$$

The energetics model is available in a computerized form (Fish Bioenergetics 3.0, Hanson et al. 1997). We modified two main processes of the original model. First, we estimated the actual consumption per time step as a species-specific feeding rate (N) which was calculated using a type-II-functional response (Holling 1959):

$$N = b_1 \times P \cdot (b_2 + P)^{-1} \quad (2)$$

where b_1 represents the maximum consumption rate (ind·min^{-1}), P represents prey density (ind·L^{-1}), and b_2 represents the prey density (ind·L^{-1}) at which the consumption rate reaches half of its maximum. Parameters were obtained from experiments with juvenile cisco and vendace at temperatures of 8 °C and at light intensities of 0.05 lux (Ohlberger et al. 2008*a*). This illumination level can be found at the daytime depth at which coregonids occur in Lake Stechlin (see below), and we used this level as an approximation of the illumination experienced within the antipredation window by the coregonids during ascent and descent. Accordingly, feeding rates mimicked the

consumption of fish at naturally observed light levels and prey densities.

Further, we calculated a fish mass-dependent stomach capacity determined for sockeye salmon (*Oncorhynchus nerka*; Brett 1971*b*) to prevent fish from feeding after the stomach capacity was reached. To determine the energy intake in each time step, we used the amount of digested food (instead of consumed food) per time step, because the low temperatures in the hypolimnion may limit digestion more strongly than consumption. We applied an exponential digestion function (Elliott and Persson 1978):

$$(3) \quad D = (M_0 - Cm \cdot r^{-1})[1 - \exp(-rt)] + Cmt$$

where D represents the amount of digested food during time t (min), M_0 represents initial stomach content mass (g wet mass), C represents the number of consumed prey, and m represents the wet mass (g) of an individual prey item. The temperature-dependent gastric evacuation rate (r, h^{-1}) for sockeye salmon was obtained from Brett and Higgs (1970):

$$(4) \quad r = 0.04 \exp(0.1T)$$

Respiration costs were calculated as a function of fish mass, temperature, and activity

$$(5) \quad R = \mathrm{RA} \cdot W^{\mathrm{RB}} \cdot f(T) \cdot \mathrm{ACT}$$

where R represents the specific rate of respiration converted into mass ($g \cdot g^{-1} \cdot d^{-1}$), W represents fish mass (g), RA represents the intercept of the allometric mass function ($g \cdot g^{-1} \cdot d^{-1}$), RB represents the slope of allometric mass function, $f(T)$ is a temperature-dependence function, T represents water temperature (°C), and ACT represents the activity multiplier. The specific rate of respiration in energy units ($J \cdot g^{-1} \cdot d^{-1}$) was obtained using the oxycaloric factor (3241 cal·g^{-1} O_2, 1 cal = 4.1868 J). The activity multiplier varied with the size-dependent swimming speed of fish (Table 1), and ranged between 1.21 and 1.36 in our model. Swimming speed was considered to be independent of temperature, because in situ observations of swimming activity of vendace indicated that swimming speed was primarily triggered by illumination strength (maximum speed during crepuscular periods, swimming speed close to zero at darkness) despite variable environmental temperatures (Gjelland et al. 2004, 2009).

Energetic waste losses through egestion and excretion were modeled by constant proportions of 0.25 or 0.1 of digested food, respectively (Kitchell et al. 1977; Rudstam et al. 1994). Specific dynamic action (SDA), which accounts for the proportional costs of digestion, was set to 0.17 (Rudstam et al. 1994). (For a detailed overview of all parameters, see Table 1.)

Empirical data

Empirical data on migration amplitudes, diet composition of fish, and vertical gradients of environmental factors were obtained from monthly sampling of the meso-oligotrophic Lake Stechlin (surface area 4.3 km^2, mean depth 22.8 m, maximum depth 68 m) from March through December 2005. The night-time depths of cisco and vendace were determined by stratified midwater-trawl catches (Helland et al. 2007) (Table 2). Daytime population depths were estimated from hydroacoustic surveys (Mehner et al. 2007; Busch and Mehner 2009). Because there was little seasonal variation, daytime depth was fixed to 35 m in the model. Duration of migration periods at dusk and dawn were calculated from the in-situ measured constant fish vertical migration speed (about 0.38 $cm \cdot s^{-1}$), and accordingly, varied between 60 and 120 min in response to seasonally varying migration amplitudes (Mehner 2006*a*; Busch and Mehner 2009).

Monthly growth rates of coregonids were estimated from the change in average size (standard length, SL, in mm) per cohort in the trawl catches. Length of fish was converted into wet mass (W, in g) using species-specific SL–W regressions for vendace ($W = 7 \cdot 10^{-6}$ $SL^{3.0683}$, $N = 3720$, $R^2 = 0.94$) and cisco ($W = 4 \cdot 10^{-6}$ $SL^{3.2324}$, $N = 588$, $R^2 = 0.87$).

Both coregonids are pelagic planktivores, and feed primarily on *Bosmina coregoni*, *B. longirostris*, *Leptodora kindtii*, and a few other cladocerans and copepods, which occur with differing densities at all depths between 0–40 m (except *L. kindtii*, which was only occasionally found below 20 m) (Helland et al. 2008). There was little trophic difference between vendace and cisco, but species-specific differences in occupied depths at night may induce slightly varying diet compositions of both coregonids for a few prey groups (e.g., *L. kindtii*) (Helland et al. 2008). Zooplankton density was estimated from vertical hauls with zooplankton nets in five different depth strata (0–10 m, 10–20 m, …, >40 m) during the daytime and at night (Helland et al. 2008). Average lengths (mm), dry mass (µg dm), and energy densities ($J \cdot g^{-1}$) of the zooplankton groups were calculated from published equations (Cummins and Wuycheck 1971; Rosen 1981; Culver et al. 1985). We used a dry mass : wet mass ratio of 4% for *L. kindtii*, and 11% for all other prey species/groups (Cummins and Wuycheck 1971). Owing to selective feeding and seasonal variation in prey species composition, we calculated the average mass and energy densities of the plankton organisms in the diet by using the relative proportions of taxa found in the stomachs of fish (Table 2).

Water temperature was continuously recorded, by temperature loggers fixed in the lake, every 30 min from the surface to 20 m, in 2 m intervals, and at 30 m. Seasonally variable vertical profiles of illumination were modeled. We used the local surface illumination I_0 at Lake Stechlin obtained from a global illumination model (sky condition 1 for maximum possible illumination: sun/moon visible, sky < 70% overcast; Janiczek and De Young 1987) and estimated illumination at depth z (m) according to the Lambert–Beer equation:

$$(6) \quad I_z = I_0 \cdot \exp(-kz)$$

where I_z represents the illumination at depth z in lux, I_0 represents the illumination at the water surface in lux, and k represents the vertical extinction coefficient. The value of k was calculated from Secchi depth (SD in m), measured twice per month in Lake Stechlin, using an equation established by Koschel (1985):

$$(7) \quad k = 0.88\ \mathrm{SD}^{(-0.416)}$$

The duration of the daily feeding period may have been constrained by the illumination level at the depths occupied by vendace and cisco. A minimum threshold of approximately 0.01 lux for visual feeding has been suggested by Dembinski (1971) and Gjelland et al. (2009). Our own ex-

Table 1: Overview of parameters of the bioenergetics-based foraging model for fish species vendace and cisco, with values, units, and sources.

Parameter	Equation	Value vendace/cisco	Source
Consumption			
b_1, maximum consumption rate (ind·min^{-1})		6.77/7.66 (<0.5 lx), 41.85/33.84 (<5 lx)*, 47.43/35.16 (>5 lx)*	1
b_2, prey density of half maximum consumption rate (ind·L^{-1})		2.27/4.06 (<0.5 lx), 2.86/2.62 (<5 lx)*, 1.85/1.51 (>5 lx)*,	1
P, prey density (ind·L^{-1})			
N, number of consumed prey (ind·min^{-1})	$b_1 \cdot P \cdot (b_2+P)^{-1}$		
SC, stomach capacity (wm, g)	$W(14.1-4.95 \log_{10}(W))/100$, for W<253.5 g		2
Digestion			
r, digestion coefficient	$0.04 \exp(0.17T)$		4
M_0, initial stomach content mass			
C_m, mass of prey eaten			
t, model time steps (min)			
D, digestion (J·t^{-1})	$[(M_0 - C_m/r) \times [1-\exp(-rt)] + (C_m t)]ED_{prey}$		3
T, temperature (°C)			
Respiration			
RA		0.0022/0.0027	5
RB		–0.21/–0.46	5
RQ, approximates the Q_{10}		0.071/0.103	5
$f(T)$, temperature dependence function	$\exp(RQ \cdot T)$		
RTO, coefficient for swimming speed dependence on metabolism (s·cm^{-1})		0.021/0.017	5
VEL, swimming speed (cm·s^{-1})	$7.23W^{0.25}$		6
ACT, activity multiplier	exp(RTO·VEL)		
R, respiration (g·g^{-1}·t^{-1})	$RA \cdot W^{RB} \cdot f(T) \cdot ACT$		
Egestion			
F, egestion (J·t^{-1})	$0.25D$		6
Excretion			
U, excretion (J·t^{-1})	$0.1 \cdot (D-F)$		6
Specific dynamic action			
SDA (J·t^{-1})	$SDA \cdot (D-F)$		6
Energy density			
ED_{prey} (J·g^{-1} wm)			
ED_{pred} (J·g^{-1} wm)	$5083+32.4W$		7

Note: Sim, simulation; Sim5, simulation with no downward migration; *, Sim5 only; ind., individuals; RA, intercept of the allometric mass function (g·g^{-1}·d^{-1}); RB, the slope of allometric mass function; wm, wet mass; (1) Ohlberger et al. 2008*a*; (2) Brett 1971; (3) Elliott and Persson 1978; (4) Finstad 2005; (5) Ohlberger et al. 2008*c*; (6) Rudstam et al. 1994; (7) Gjelland 2008.

periments showed that both coregonid species fed with reduced efficiency at 0.05 lux, and completely cease feeding at 0.005 lux (Ohlberger et al. 2008*a*). Therefore, we assumed that fish stopped feeding if illumination in the occupied habitat dropped below 0.01 lux. The nonfeeding period thus extended from approximately the middle of the ascent at dusk till the middle of the descent at dawn, whereas there was sufficient light (0.5 lx > I_z > 0.01 lx) for feeding throughout the daytime period in deeper water layers.

Simulations

We simulated individual fish that represent cohorts from both species with comparable fish masses (vendace age class 1: 5.37 g; cisco age class 2: 6.00 g) obtained from catches at the end of March 2005. These fish masses were used as start mass for all seasonal simulations. Fish masses in consecutive months were determined by adding a total mass increment per month (g) to the initial mass. Standard simulations applied time steps of 5 min (288 time steps within 24 h). In a 24-h cycle, four periods were distinguished during which the fish occupied a given vertical habitat. Fishes occurred in deep-water habitats during the day and in shallow-water habitats during the night, with exact depths (m) taken from our empirical results (Table 2). Ascent and descent between both habitats occurred at dusk and dawn, respectively. Each habitat was characterized by water temperature (°C) and overall zooplankton abundance (ind·L^{-1}), as well as the average wet mass (µg wm) and energy density (J·g^{-1} wm) of dominant prey. For the crepuscular migration periods, mean values of environmental factors from the day and night habitats were applied.

In each time step, the fish consumed food depending on prey density if illumination was above the 0.01 lux threshold. Fish growth in each time step was determined by subtracting energetic losses from the energy obtained from digested food.

Table 2. Environmental inputs used in modeling diel vertical migration scenarios for vendace (v) and cisco (c) or both (v/c) during 9 months in 2005 in Lake Stechlin, Germany.

	Observed depth (OD) (m)		Zooplankton density (ind·L^{-1})			Prey mass (µg, wm)		Prey energy density (J·g^{-1})		Feeding duration in 24 h (min)			
			OD		35 m					Sim1–3	Sim4	Sim5	
	v	c	v	c	v/c	v	c	v	c	v/c	v/c	v	c
18 Apr.	14.4	28.8	16.9	16.6	5.0	36.5	35.7	2596	2575	920/860	840	970	870
23 May	16.3	25.5	9.0	5.7	6.0	62.1	43.8	1696	2709	910	860	1050	990
13 June	14.5	28.4	11.7	5.2	2.4	116.9	75.5	1675	2793	980	900	1120	1030
18 July	16.6	19.1	18.7	18.2	6.3	541.2	525.1	950	955	950	930	1070	1050
9 Aug.	13.1	13.1	24.9	24.9	7.5	528.4	321.7	963	1026	870	800	990	990
21 Sept.	15.9	21.9	17.0	10.9	3.0	417.0	230.4	1001	1821	710	670	760	770
17 Oct.	18.1	21.4	10.9	8.9	3.9	25.5	37.3	2512	2533	610	560	690	670
14 Nov.	19.5	25.8	6.4	4.5	1.3	73.6	52.4	2784	2705	540	460	580	550
13 Dec.	15.3	24.5	4.6	4.2	2.0	42.7	37.7	2688	2671	480	440	550	500

Note: OD, observed depth occupied by predators at night, as estimated from depth-stratified midwater trawl sampling. Sim1–3, simulations 1–3; Sim1, migration amplitudes, prey densities, and temperatures are completely matched to those observed in Lake Stechlin in 2005; Sim2, occupied depths were shifted 5 m upwards relative to the empirically determined depth; Sim3, occupied depth was shifted 5 m downwards; Sim4, simulation with no upward migration; Sim5, simulation with no downward migration.

Any undigested food in the stomach of the fish at the end of the time step was carried over to the next time step. Food consumed in the next time step was then added to the undigested food in the stomach. If the amount of consumed food during a time step exceeded the stomach capacity of the fish, consumption was limited to stomach capacity. This procedure was repeated for all 288 time steps (24 h). Finally, daily growth is calculated by adding up the growth rates from all time steps. Each 24 h period was repeatedly simulated until the system reached a steady state (Bevelhimer and Adams 1993) where the end stomach content equaled the initial stomach content. This was done because the initial stomach content of a fish is generally determined by the final stomach content from the previous day, and should therefore be equal. We ran one simulation per month based on environmental conditions and estimated daily values for growth (g), respiration (kJ), and consumption (g), and then multiplied the daily output by the number of days in a month to obtain monthly estimates.

The parameterized model for vendace and cisco was not calibrated or fitted to any dataset. For model validation, we ran a first scenario (Sim1: OD) that completely matched the migration amplitudes, prey densities, and temperatures observed in Lake Stechlin in 2005. The growth rates obtained from this scenario were compared with the empirically observed growth rates of coregonids from Lake Stechlin in 2005, which were independent of the model's parameterization. This was done by plotting modeled versus observed fish masses per month, calculating the coefficient of determination (R^2) of the linear regression between observed and predicted fish masses, and calculating a dimensionless measure of modeling efficiency (EF):

$$(8) \qquad EF = 1 - \frac{\sum (y_0 - y_p)^2}{\sum (y_0 - y_m)^2}$$

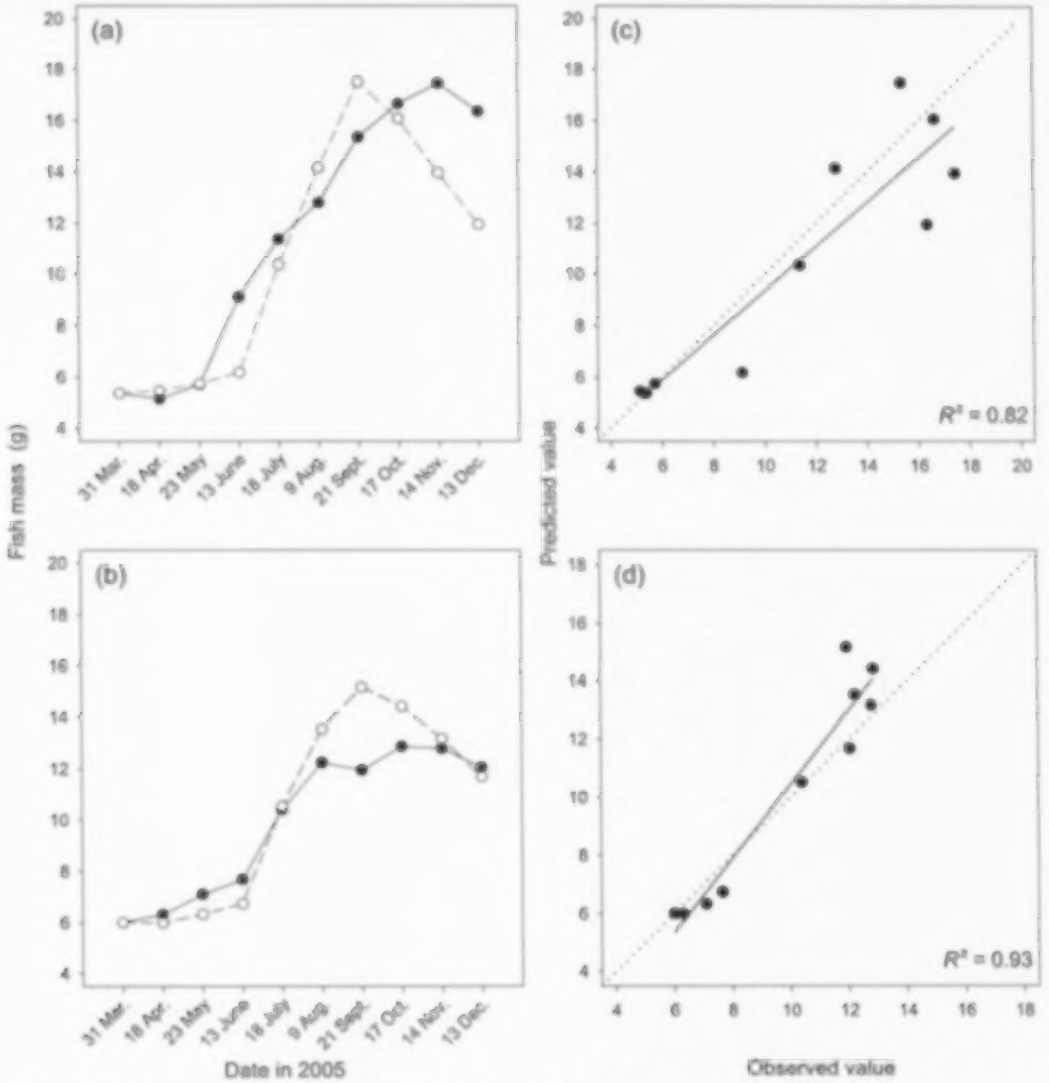
where y_0 represents the observed value, y_p represents the predicted value, and y_m represents the mean of observed values (Mayer and Butler 1993). Slopes and intercepts of the regression between observed and modeled fish masses were tested for deviation from unity, using R software version 2.10.1 (R Development Core Team 2005) and working package "smatr" version 2.1 (Warton 2007). Mass data were normally distributed (Kolmogorov–Smirnov) and passed the Levene-test for homogeneity of variance.

To elucidate the details of the balance between feeding rates and respiration costs in the respective habitats occupied each month, we ran several scenarios in which we modified migration amplitudes by shifting the occupied depths at night. To check for the sensitivity of the depth occupied at night, we shifted the occupied depths 5 m upwards relative to the empirically determined depth (Sim2: OD – 5), or alternatively 5 m downwards (Sim3: OD + 5). In the final two scenarios, the occupied depth was kept constant at 35 m (no upward migration; Sim4: OD_{deep}) or fish occupied the observed night-time depths over the diel cycle (no downward migration, Sim5: $OD_{shallow}$). For comparison of model scenarios, total growth of an individual fish over 9 months (g) was calculated from daily mass increments. Specific respiration rates (kJ·g^{-1}·d^{-1}) were compared among scenarios, and the mean temperatures at night-time depths of vendace and cisco over 9 months were estimated. The model was generated as a macro script in a MS Excel® routine written in VBA (Visual Basics for Applications). All calculations were performed using PASW 17.0 if not stated otherwise (SPSS Inc., Chicago, Illinois, USA).

Results

The standard scenario run by our reparameterized model reasonably reproduced the growth of individual vendace (Fig. 1*a*) and cisco (Fig. 1*b*) between March and December 2005. The coefficients of determination of the linear regressions between observed and predicted masses of fish per month (vendace: Fig. 1*c*, $R^2 = 0.82$, $p < 0.001$, $N = 10$; cisco: Fig. 1*d*, $R^2 = 0.93$, $p < 0.001$, $N = 10$) and the modeling efficiency (EF: vendace 0.78; cisco 0.77) were further evidence of the good fit between the model and the empirical data. The slopes (m) of the linear regressions did not differ from one for vendace ($m = 0.86$, slope-test: $r = -0.32$, $p = 0.37$) and cisco ($m = 1.27$, $r = 0.61$, $p = 0.06$). Similarly, the intercepts (n) showed no deviation from zero for vendace

Fig. 1. Fish mass (g) of (*a*) vendace and (*b*) cisco observed (filled circles) in the field between March and December 2005, and values predicted (open circles) by the bioenergetics model. Predicted fish mass based on the bioenergetics model for (*c*) vendace and (*d*) cisco as a function of observed fish mass derived from field data. The unbroken line represents the regression line fitted to the points. R^2 is the proportion of variance explained by the linear regression model. The broken line represents a theoretical line with a slope of unity.

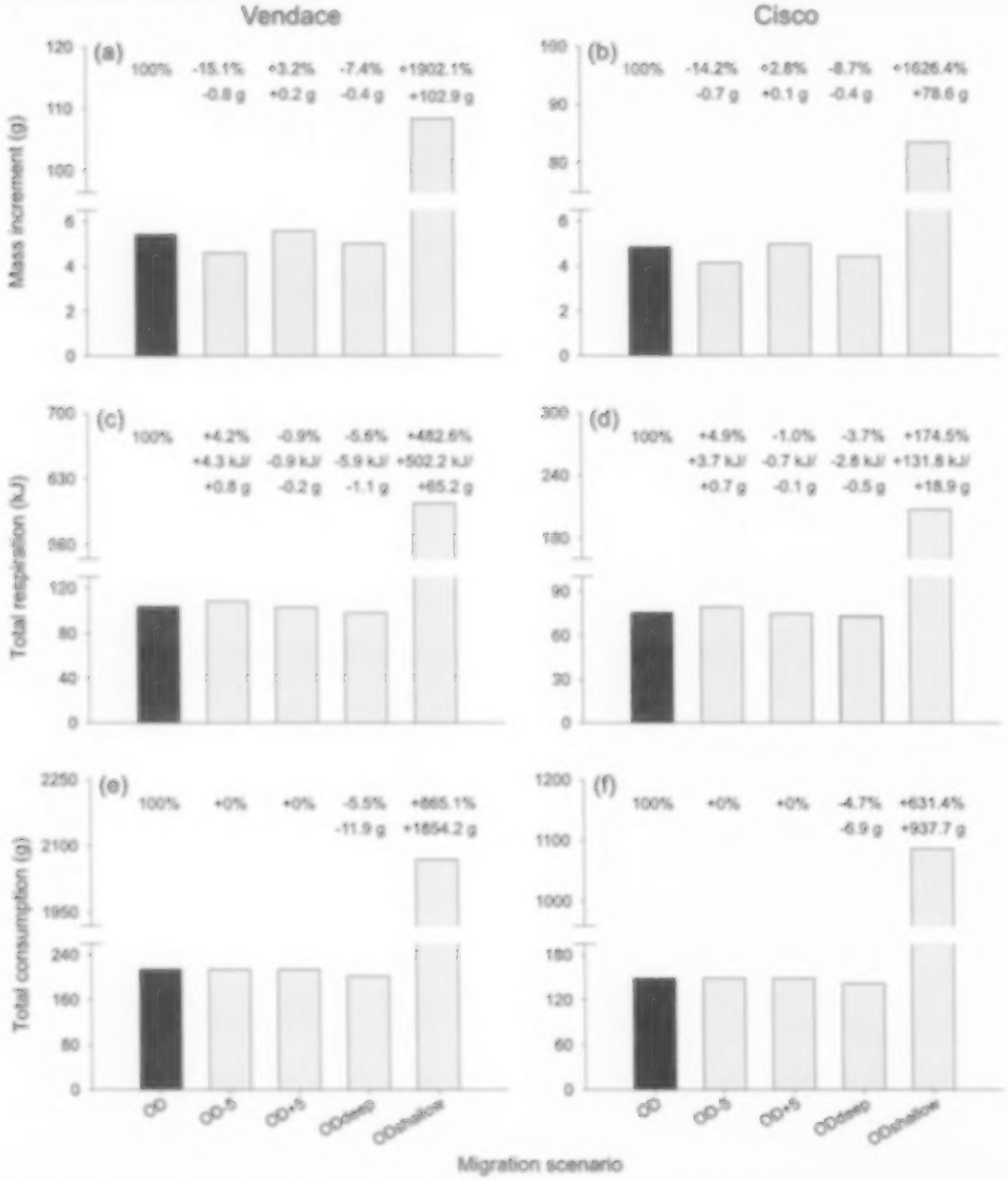


(n = 0.72, elevation test: t = 0.40, p = 0.70) and cisco (n = –2.30, t = –1.77, p = 0.11).

In the first simulation (Sim1), we calculated total growth (5.41 g; 4.84 g), total respiration (104.06 kJ; 75.50 kJ) and total consumption (214.34 g; 148.50 g) over 9 months for vendace and cisco, respectively. Mean temperatures at the occupied depths over 9 months were 6.1 °C for vendace and 5.7 °C for cisco. These results acted as the reference values for further simulations (Sim2–Sim5).

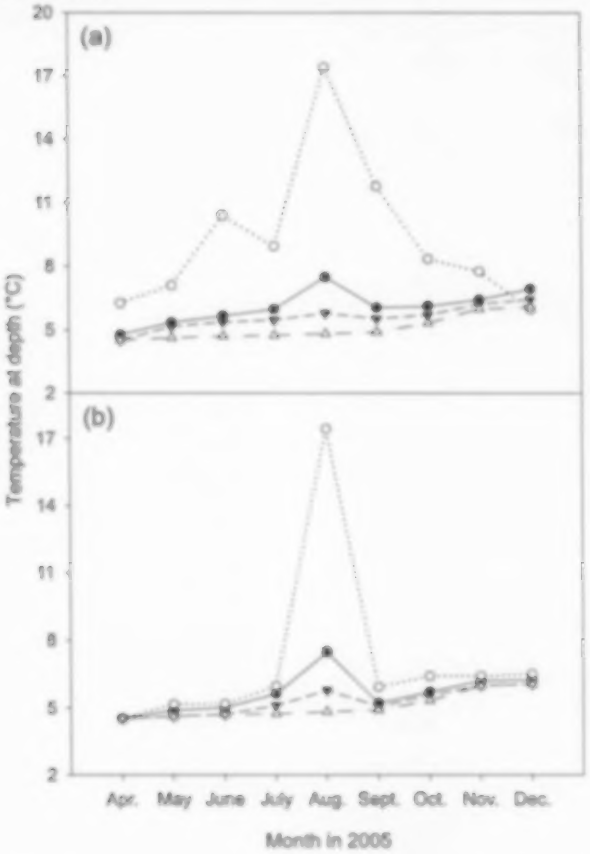
Further simulations revealed a high sensitivity of the model to the depths occupied at night. If fish migrated into shallower depths at night (Sim2: OD – 5 m), total growth relative to Sim1 was reduced by 15.1% in vendace (Fig. 2*a*) and by 14.2% in cisco (Fig. 2*b*). In contrast, the total mass increment increased by 3.2% for vendace and 2.8% for cisco when we simulated occurrence in slightly deeper water at night (Sim3: OD + 5 m, Fig. 2). The sensitivity of total growth to the depth occupied at night was primarily caused by the temperature dependence of respiration. The temperatures experienced at night were substantially higher in Sim2, and slightly lower in Sim3 when compared with the observed scenario (Figs. 3*a* and 3*b*). Accordingly, the specific respiration rates were 4.2% higher for vendace and 4.9% higher for cisco if fish occurred in shallower water at night (Figs. 2*c* and 2*d*; Sim2). The modeled changes in depth distribution at night (Sim2–Sim3) did not affect the consumption rate of either species, because illumination levels in night-time habitats were below the threshold of 0.01 lux and thus fish had ceased feeding. Hence,

Fig. 2. Comparison of mass increment (g), total respiration (kJ), and consumption (g) of (*a*, *c*, *e*) vendace and (*b*, *d*, *f*) cisco over 9 months for simulation scenarios differing in occupied depths (OD, m) at night and migration strategies. Sim1 (OD, black column) acts as a reference and the total value was set to 100%. Numbers on top of the grey columns (Sim2–Sim5) show the deviation from the reference value as percentages and absolute values (g and kJ, respectively).



average consumption over 9 months was identical in all simulated scenarios with variable migration amplitudes (Sim1–Sim3) for vendace (0.089 ± 0.0009 $g \cdot g^{-1} \cdot d^{-1}$; mean ± SD) and cisco (0.063 ± 0.0003 $g \cdot g^{-1} \cdot d^{-1}$). The effect of nighttime depth on digestion was minor and negligible, since fish never filled their stomachs to the maximum capacity. On average, the predicted percentage of stomach capacity filled at night over 9 months (Sim1) ranged from 0.30% (October) to 21.38% (December) for vendace and from 0.44% (December) to 18.80% (July) for cisco. These predicted values were not significantly different from maximum observed values over 9 months for vendace (field: 0.21% (December) to 14.13% (July); independent *t* test: $t_{[16]} = 0.73$, $p = 0.48$) and cisco (field: 0.01% (December) to 9.38% (July); inde-

Fig. 3. Scatter plot of mean monthly temperatures at population depths (occupied depths (OD), filled circles; OD – 5, open circles; OD + 5, filled triangles; 35 m depth, open triangles) of (*a*) vendace and (*b*) cisco.



pendent *t* test: $t_{[16]} = 0.84$, $p = 0.41$), which were calculated from stomach fullness in the same way as in the model.

Without DVM, the total growth of coregonids was mainly determined by the length of the feeding period and the consumption rate. Fishes occupying the hypolimnetic habitat over the diel cycle (Sim4, OD_{deep}) grew less (vendace –7.4% and cisco –8.7%) by comparison with our reference with DVM, despite lower respiration costs (vendace –5.6%, cisco –3.7%, Fig. 2). The reduction in growth was attributable to shorter feeding durations and reduced total consumption (vendace –5.5%, cisco –4.7%, Fig. 2) in deeper waters. Nonmigratory fishes that occupied metalimnetic depths throughout the diel cycle (Sim5, $OD_{shallow}$) experienced a dramatic increase in growth. Growth was about 19× (vendace) and 16× (cisco) higher compared with the reference values. Growth was maximized as a result of higher consumption (9-fold for vendace and 6-fold for cisco compared with the reference values) caused by prolonged feeding above the threshold light intensities, higher feeding rates at higher illumination, and overall higher prey densities in shallower waters. Respiration of fish was also higher (5-fold for vendace and 1.7-fold for cisco) in warmer waters, but these costs were compensated for by the higher consumption.

Discussion

Our simulations revealed that the bioenergetics model parameterized with experimentally obtained feeding and respiration rates for vendace and cisco from Lake Stechlin reasonably reproduced the empirically observed growth rates of both species for nine consecutive months. The good match between model predictions and actual growth rates was not self-evident, because the behavioral patterns of fish with temperature-dependent amplitudes of diel vertical migrations added complexity to the usual application of bioenergetics to populations occupying one habitat only. The results further demonstrate that even modest variability in the night-time population depths and hence migration amplitudes may cause substantial changes in growth rates of fish, suggesting that the habitat choice of fish at night has important energetic implications. Finally, our simulations reflect that in terms of bioenergetics, DVM is only a moderately efficient strategy. Whereas DVM is clearly more profitable than strategies with static occurrence in hypolimnetic layers, permanent residence in metalimnetic water would result in the highest growth rates of the fishes by far. Contrary behavior suggests that other factors, such as spatio-temporal gradients of predation risk (real or past), may also be operating (Johnston 1990; Hrabik et al. 2006). In combination, our results support the view that DVM of fishes in deep, stratified lakes may be an outcome of the complex interplay among mechanisms and processes related to the simultaneously occurring vertical gradients of light, temperature, zooplankton density, and predation risk.

We reparameterized an existing bioenergetics model (Stockwell and Johnson 1997, 1999) with experimentally determined feeding and respiration rates for the coexisting coregonids in Lake Stechlin (Ohlberger et al. 2008*a*, 2008*b*, 2008*c*). Physiological segregation between vendace and cisco along the vertical abiotic gradients may have contributed to the presumed sympatric speciation of the species pair (Ohlberger et al. 2008*b*). Accordingly, the validation of the results from the bioenergetics model by empirical data had to match seasonally variable, species-specific behavioral patterns. The reasonably good agreement of modeled and observed growth rates for both vendace and cisco support that bioenergetics models are most sensitive to the application of species-specific consumption and respiration rates (Rice and Cochran 1984; Hansen et al. 1993; Ney 1993). Nevertheless, a few further details decisively influenced the simulations.

The light threshold for foraging was critical for all model simulations. We implemented a minimum light threshold such that fish stopped feeding at illumination below 0.01 lux, thus limiting the length of the daily feeding period according to the depth distribution of coregonids. Therefore, coregonids fed continuously throughout the day in the deeper habitat and partly during their upward and downward migrations, but stopped feeding at night. Experiments under controlled illumination and with zooplankton densities similar to those in Lake Stechlin (up to 8 ind·L^{-1}) suggest that efficient feeding of vendace and cisco is impaired below 0.05 lux, and stops at 0.005 lux (Ohlberger et al. 2008*a*). These experiments support our chosen illumination threshold and let us conclude that coregonids do not feed at night. A similarly low illumination threshold of 0.01 lx has been suggested for

feeding of vendace in other lakes (Dembinski 1971; Gjelland et al. 2009). In contrast, other salmonid species were reported to feed under complete darkness, although feeding efficiency and selectivity were reduced (Janssen and Brandt 1980; Link and Edsall 1996; Koski et al. 2003). Stomach content analysis of larval lake whitefish (*Coregonus clupeaformis*) in Lake Ontario suggested that feeding over 24 h was continuous, but more intense during day than at night (Johnson et al. 2009). Therefore, we cannot exclude that foraging of coregonids in Lake Stechlin continues at illumination levels below 0.01 lux. However, it is unlikely that the food intake during darkness is substantial, as indicated by recent studies on alewife (*Alosa pseudoharengus*) (Boscarino et al. 2010). This conclusion is supported by the fact that the modeled growth rates were comparable with empirical rates, despite applying the illumination-constrained feeding period in which no feeding occurred during darkness.

The costs of vertical migrations were not fully considered. Although our model accounted for mass-dependent swimming costs by adding activity expenditures to respiration, the costs for swim bladder compensation were neglected. The few studies available suggest very low total migration costs in DVM of fish (Bevelhimer and Adams 1993; Strand et al. 2005), and therefore it is unlikely that the main conclusions from our comparative simulations would have changed if we considered realistic migration costs. Costs for reproduction or energetic losses due to spawning were also not specifically considered. But since growth was expressed as changes in mass, we argue that the costs of reproduction were indirectly accounted for by the mass increment of individual fish. A final objection to the model may arise from simulating zooplankton prey as a nondepletable resource. Accordingly, coregonids were modeled to feed during the illuminated periods at a rate determined by the empirically observed average zooplankton density. The assumption of nondepleted prey densities is justified by the fact that the abundance ratio between zooplankton and coregonids (total of all size classes) in the hypolimnetic layers was on average 120 000 across the monthly samplings in 2005 (T. Mehner, unpublished data). The maximum daily consumption estimated from our model was about 4800 (vendace) and 4500 (cisco) zooplankton individuals, thus suggesting that if all fish were of similar age as those in our model that they would use less than 4% of the available zooplankton per day.

Our model demonstrated that even small simulated changes in night-time OD (OD $\pm$ 5 m) caused substantial modifications of growth rates of coregonids. This sensitivity of the model is entirely attributable to the temperature dependence of respiration costs, because at night, fish occur at depths that are too dark to allow for efficient feeding. During stratification of Lake Stechlin, vendace and cisco are found in isothermal layers whose vertical locations are determined by the location and extension of the thermocline (Busch and Mehner 2009; Mehner et al. 2010). Our bioenergetics simulations elucidate that the occurrence in this layer is an energetic compromise relative to even modest ($\pm$5 m) shifts in occupied depths. On the one hand, water temperature would increase steeply if fish occurred only a few metres above their preferred OD and the respiration costs would likewise increase substantially. On the other hand, the occurrence in layers a few metres below the preferred OD would not increase the growth rates, because the weak temperature gradient below the metalimnetic layers would result in respiration costs almost identical to those estimated for the occurrence at the OD.

Nevertheless, the ascent from the hypolimnetic into metalimnetic layers at night has energetic benefits, because the increased consumption rates along the vertical gradient of zooplankton density outweigh the increasing costs of respiration in the warmer water. The simulation with permanent residency in hypolimnetic layers (OD_{deep}) shows that growth rates of vendace and cisco would decline by approximately 7% and 9%, respectively. These reduced growth rates occur despite continuous feeding during daytime periods and lower respiration costs in the cold, 4–5 °C water. Furthermore, vendace grew faster than cisco, despite the fact that both coregonids have widely similar trophic niches (Helland et al. 2008) and feeding efficiencies (Ohlberger et al. 2008*b*). Obviously, there is a species-specific balance between respiration costs and feeding gains that explains the differing energetic profitability of DVM in vendace and cisco. Temperature is an important factor for segregating species that differ in optimum temperature (Crowder et al. 1981). Ohlberger et al. (2008*b*) found evidence for competing temperature-related physiological strategies. Cisco show a reduced standard metabolism at temperatures ranging from 4–15 °C compared with vendace. Furthermore, cisco experience lower active metabolic costs than vendace at lower temperatures (<8 °C), whereas vendace are energetically more efficient than cisco at higher temperatures (≥8 °C). Accordingly, cisco have lower relative respiration costs than vendace during daytime. During the crepuscular and night-time periods, however, vendace ascend into layers with optimum temperature, thus reducing the respiration costs relative to daytime.

Furthermore, feeding rate is another important factor influencing the competitive ability of organisms (Mittelbach 1981). The feeding efficiency of vendace and cisco contributes to the species-specific differences in consumption and growth. Although the maximum prey capture rate is slightly higher for cisco, vendace is a more successful predator with about 13% higher capture rates than cisco at low prey densities (<11.5 ind·L^{-1}), owing to the lower half-saturation constant (b_2) of its functional response curve. Furthermore, vendace feeds on prey items with larger body masses compared with cisco (on average 36%). Owing to the larger migration amplitude of vendace relative to cisco, vendace can feed during ascent on the profitable prey *L. kindtii*, which occur mainly in metalimnetic waters. In contrast, the preference of cisco for layers with metabolically optimum temperatures around 4–5 °C during ascent and descent limits access to *L. kindtii* during ascent and descent, and hence the consumption and growth rates of cisco are lower than those of vendace, particularly during the summer months between June and September, when *L. kindtii* is abundant (Helland et al. 2008). This suggests that the lower growth of cisco as compared with vendace is entirely attributable to a less optimal balance between feeding gains and respiration costs in their preferred habitats, and not a result of lower conversion efficiencies, as suggested for other dwarf coregonid species (Trudel et al. 2001). Furthermore, our results for both coregonid species are consistent with similar calculations that in bioenergetic terms, DVM is adaptive compared with continuous occurrence in cold, deep waters where low feeding and

growth rates would produce competitively inferior individuals (Bevelhimer and Adams 1993; Jensen et al. 2006).

Surprisingly however, our simulations suggested that DVM is not the most energetically efficient strategy. Coregonids staying in metalimnetic waters over the diel cycle ($OD_{shallow}$) would have a dramatic growth advantage relative to any alternative strategy. The gross food conversion efficiency (K; grams of growth·(grams of food consumed)$^{-1}$, Winberg 1956) over 9 months was determined for Sim5 to demonstrate that the predicted growth rates were not unrealistic. We calculated K-values of 29% (vendace) and 39% (cisco). These results were in accordance with experimentally obtained K-values of 33% for coregonids that were fed ad libitum at low temperatures (8 °C) (Mehner et al. 2011). This growth advantage was caused by the greatly enhanced feeding rates at higher illumination strengths, higher zooplankton densities, and longer feeding periods in shallower waters, which more than compensates for the higher respiration costs in the warmer water. This result contradicts a number of studies that have demonstrated a bioenergetics advantage of DVM over any other strategy of diel habitat choice (Wurtsbaugh and Neverman 1988; Bevelhimer and Adams 1993; Sims et al. 2006). However, it must be considered that coregonids staying permanently in the metalimnetic waters may eventually deplete their prey resources, because they will consume 6–9× more zooplankton than while performing DVM. Although monthly mean zooplankton density was on average about 3× higher in the shallow layers than in the deep layers, this difference might not be large enough to compensate for a 9× higher consumption rate. We did not model potential depletion of resources in Sim5, owing to the added complexity, but suggest that the relative performance of resident vs. migrating strategies may critically depend on the exact quantification of the exploitation rates of prey resources, in particular if extremely high feeding rates by the fish are assumed.

The simulations suggest that the coregonids were not employing a strategy to maximize growth, but instead seemed to balance tradeoffs between growth and potential predation risk. Migrating deeper at dawn should confer decreased predation risk by visually hunting piscivores (Scheuerell and Schindler 2003; Hrabik et al. 2006). Pike (*Esox lucius*) and perch (*Perca fluviatilis*) are piscivorous predators in the fish community of Lake Stechlin, in which pike is mainly bound to the littoral zone of the lake (Anwand et al. 2003). Perch is the only predator that co-occurs with vendace and cisco in the upper pelagic area. However, numerous fishing campaigns in Lake Stechlin, including, pelagic gillnets over 8 months in 2000 (Mehner and Schulz 2002; Mehner et al. 2010), annual midwater trawls since 2002 (Mehner 2006*b*; Helland et al. 2007) and echosounding over 10 months in 2005 (Mehner et al. 2007), revealed that the number of perch is only a minor fraction (0.0%–1.3%) of the total pelagic fish density (see Mehner et al. 2010). The density of aerial fish predators such as cormorants (*Phalacrocorax* spp.) and crested grebes (*Podiceps cristatus*) is likewise low in Lake Stechlin (Mehner et al. 2007). Nevertheless, it is conceivable that the chemical cues from even a few predators in the epilimnion could stimulate migration behavior, despite very infrequent encounters between piscivores and their prey fishes. A similar explanation has been suggested for behavior of migrating young-of-the-year burbot (*Lota lota*) and other coregonid species (*C. artedi*, *C. lavaretus*, *C. albula*) (Gjelland et al. 2009; Probst and Eckmann 2009; Stockwell et al. 2010). These studies have all concluded that the chemical presence of predators may drive DVM in prey fish, despite little evidence for direct predation mortality.

Our calculations support the view that the ultimate causes of DVM in Lake Stechlin coregonids may be a mixture of energetic costs (respiration) and benefits (feeding rates), and the experienced or perceived predation risk in alternative habitats (multifactor hypothesis). Predation and light both place time constraints on the foraging of coregonids. During the daytime, predators restrict coregonids to deeper, darker habitats, where prey density is low, and at night, when coregonids can safely move to shallower food-rich water layers, decreasing light intensities limit feeding to the short periods during upward and downward migration. While predation is the dominant factor during the daytime, food availability and energetic expenditures seem to dominate at night. They determine the species-specific depth distribution and migration amplitudes by balancing metabolic costs and food intake. Occupied depths at night are chosen to maximize food consumption during migration periods and to minimize metabolic costs, by occurring within temperature ranges where energetic efficiency is maximized.

The motivation behind DVM, however, often changes among and within systems and species (Stockwell and Johnson 1999). In more productive systems or in lakes where animals migrate with larger amplitudes and experience a broader range of temperatures, temperature-dependent respiration is likely to become an important consideration. When food is abundant and stomach capacity limits consumption, moving to warmer water layers can be energetically beneficial (e.g., it promotes digestion and increases growth rates) (Wurtsbaugh and Neverman 1988). In less productive lakes, when food may be limited, reducing metabolic cost by resting in colder water layers could be the optimal strategy (Bevelhimer and Adams 1993). Accordingly, a single ultimate explanation may fail to address the temporal and spatial variability of DVM patterns which are usually observed in empirical studies.

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PERSPECTIVE / PERSPECTIVE

The cumulative impacts of climate change on Fraser River sockeye salmon (*Oncorhynchus nerka*) and implications for management

Michael Healey

Abstract: Anadromous Pacific salmon (*Oncorhynchus* spp.) are vulnerable to climate change in both freshwater and marine habitats. I use a qualitative model to assess the cumulative effects of climate change across life stages and generations of Fraser River sockeye salmon (*Oncorhynchus nerka*) and other salmon species. The effects of climate change most relevant to Fraser River sockeye include warming of freshwater and marine habitats, altered hydrology in spawning rivers, reduced productivity in nursery habitats, and changed distribution and phenology of predator and prey species. The weight of evidence indicates that these changes will negatively affect growth and survival of Fraser River sockeye at all life stages. Effects on one life stage will also carry forward to heighten adverse effects at subsequent life stages and across generations so that the cumulative impact is greater than the impact on individual stages. Salmon can adapt to climate change but probably not enough to sustain productivity. In the south, focus of policy and management on conserving and enhancing resilience is needed to retain some salmon production. At the same time, Arctic habitats are becoming accessible to salmon. Management in the Arctic should protect potentially productive habitats from development and facilitate their colonization by Pacific salmon.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) sont vulnérables aux changements climatiques, à la fois en milieu d'eau douce et en milieu marin. Un modèle quantitatif permet d'évaluer les effets cumulatifs des changements climatiques durant les stades du cycle biologique et au cours des générations chez le saumon rouge (*Oncorhynchus nerka*) du fleuve Fraser et chez d'autres espèces de saumons. Les effets des changements climatiques les plus pertinents pour les saumons rouges du Fraser incluent le réchauffement des habitats d'eau douce et de mer, une modification de l'hydrologie des rivières de fraie, une réduction de la production dans les habitats de nourricerie et un changement dans la répartition et la phénologie des espèces de proies et de prédateurs. Les données actuelles indiquent que ces changements vont affecter négativement la croissance et la survie du saumon rouge du Fraser à tous les stades de son cycle biologique. Les effets sur un stade du cycle vont se répercuter sur les stades subséquents et sur les générations suivantes en augmentant les effets négatifs, si bien que l'impact cumulatif sera plus important que l'impact sur les stades individuels. Les saumons peuvent s'adapter aux changements climatiques, mais probablement pas assez pour maintenir la productivité. Dans le sud, les politiques et la gestion devront cibler la conservation et l'augmentation de la résilience afin de sauvegarder une partie de la production de saumons. Au même moment, les habitats arctiques vont s'ouvrir au saumon. La gestion dans l'arctique devrait protéger les habitats productifs potentiels du développement et faciliter leur colonisation par les saumons du Pacifique.

[Traduit par la Rédaction]

Introduction

The species of Pacific salmon (*Oncorhynchus* spp.) are economically, culturally, and ecologically important throughout their North Pacific range (Healey 1993; Johnsen 2001; Naiman et al. 2002). Because of this, the effects of climate change on Pacific salmon are of major concern to resource managers (Mote et al. 2003; Mantua and Francis 2004; Schindler et al. 2008). The freshwater and marine habitats of salmon are expected to warm by 2–5 °C or more over the next century, perhaps earlier (Henderson et al. 1992; Ficke et al. 2007; Mackas et al. 2007). This degree of warming will have uncertain but potentially devastating effects on salmon and their ecosystems (Beaugrand and Reid 2003; Beamish 2008; Barange and Perry 2009). In addition, precipitation

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patterns, storm frequency and severity, distribution and phenology of food organisms and predators, and many other factors affecting salmon are expected to change with uncertain but potentially serious consequences for the species (Richardson 2008; Bryant 2009; Schwing et al. 2010).

The Fraser River in British Columbia is the most important salmon-producing river in Canada and one of the most important in North America (Northcote and Larkin 1989). Salmon have spawned in the Fraser River for thousands of years, and their annual spawning run has provided an abundant harvest for aboriginal and, more recently, commercial fishers (Johnsen 2001). Sockeye salmon (*Oncorhynchus nerka*) is the most valuable species in the Fraser River, and the sockeye harvest is shared with fishers from the USA under the terms of the Pacific salmon treaty (Roos 1991). Aboriginal communities along the Fraser River also depend on the sockeye runs to provide salmon for food and ceremonial purposes. Because of their commercial and cultural importance, sockeye salmon in the Fraser River are among the best studied of Pacific salmon. The wealth of information on this species allows me to make relatively informed judgments about the likely effects of climate change. Fraser River sockeye are thus a useful model species for understanding the effects of climate change.

Over the past century, Fraser River sockeye runs have ranged from highs of 20–30 million to lows of a few million fish (Roos 1991). Returns during the 1980s and 1990s were particularly strong owing to favourable ocean conditions (Beamish et al. 1997). In the past decade, however, some of the major sockeye runs to the Fraser River have shown anomalous timing and unusual mortality (Cooke et al. 2004). In the past few years, ocean returns have collapsed, prompting a judicial inquiry (Prime Minister's Office 2009). Paradoxically, the 2010 sockeye return to the Fraser River is one of the largest on record (CBC news: www.cbc.ca/news/canada/british-columbia/story/2010/08/25/bc-sockeye-salmon-fraser-river.html, accessed 17 March 2011). The causes of these events are unknown, but the multifaceted and cumulative effects of climate change offer one explanation (Hinch and Gardner 2009; Hague et al. 2010). An examination of the effects of climate change is timely, therefore, in terms of the ongoing management of salmon fisheries.

Various authors have examined the potential effects of global warming on parts of the salmon life cycle (Henderson et al. 1992; Hinch et al. 1995*a*; Rand et al. 2006), as well as on overall production rates (Klyashtorin 1998; Levin 2003; Beamish 2008). Crozier et al. (2008) examined the potential for phenotypic and genetic responses to climate warming among different life history stages of Chinook salmon (*Oncorhynchus tshawytscha*). To date, however, no one has explored the way changes at one life stage propagate through the life cycle to affect other stages or accumulate across generations. Here I develop such a qualitative model, emphasizing the cumulative effects of climate change on successive stages in the life cycle of Fraser River sockeye salmon. Although I develop the model in detail for sockeye salmon, it is easily adapted to other salmon species and, potentially, to other marine and freshwater fishes. I also explore the implications of the model for future salmon production and management. The paper is organized into four sections: the effects of climate change on the habitats of different life stages; biological responses by each life stage to habitat change; synthesis of cumulative effects; and potential for mitigation. I summarize life stage responses to climate change and potential for mitigation in Table 1. Although any forecast of the effects of climate change has high uncertainty, the prognosis for salmon in the southern part of their range is not good. However, there are some positive notes for salmon productivity in the northern half of their range, at least for a number of decades, and new habitats are emerging in the Arctic that may provide future opportunity if they receive the right kind of management.

Climate warming and sockeye habitats

Pacific salmon are anadromous, spawning and spending a portion of their juvenile life in fresh water but migrating to sea to complete the majority of their growth before maturity. In the Fraser River, female sockeye deposit their eggs in the late summer and autumn in gravel spawning beds distributed throughout the basin, the eggs incubate over the winter in the spawning nest, and the fry emerge in spring and typically migrate to a nearby nursery lake. After 1 or sometimes 2 years feeding and growing in the lake, fry transform to smolts in spring and migrate to sea (Burgner 1991). In a few (mainly very small) populations, fry do not migrate to a nursery lake but reside for a few months in their natal stream or nearby river delta and migrate to sea in late summer. The Harrison River population of sockeye in the Fraser River shows this behaviour pattern (Gustafson and Winans 1999). When they reach the ocean, juveniles migrate north and west in continental shelf waters until autumn, then move offshore into the Gulf of Alaska. They mature after 2 or more years at sea and return to the Fraser River to spawn (Foerster 1968; Burgner 1991). Over their life cycle, therefore, Fraser River sockeye (and other anadromous salmon species) integrate the effects of climate change across a number of freshwater and marine habitats; climate effects on one stage can carry forward to influence effects at another stage. The consequences of changes in habitat for one generation can also carry forward to influence success in subsequent generations. For the purposes of this paper, I assess climate effects on eight stages in the life of sockeye: (1) egg and alevin; (2) fry: emergence to lake entry; (3) fry: lake entry to first winter; (4) fry: first winter; (5) smolting and seaward migration; (6) postsmolts: estuary and coastal; (7) immatures in the ocean; (8) returning adults. I chose these stages to illustrate the impact of different sets of climate change factors across the life of salmon.

Global climate change is expected to result in higher average temperatures and altered precipitation and storm patterns (Mote et al. 2003; Beamish 2008; Barange and Perry 2009). Absorption of CO_2 by the ocean is also reducing the pH of oceanic waters (Fabry et al. 2008). The degree of future change in these variables is uncertain, but under a "Business As Usual" scenario over the next century, air temperatures in the Fraser basin will increase between 2 and 5 °C. Increases will be greater in winter than in summer and greater further north and at higher elevations (Melack et al. 1997; McDaniels et al. 2010). Sea surface temperature (SST) in the Gulf of Alaska will increase by 2–4 °C, and the increase will be greater near the coast than offshore (Mackas et al. 2007). In

Table 1. Effects of global warming and the potential for mitigation–adaptation (in terms of the biological response of the fish, direct management action, or modification of policy) among life cycle stages of sockeye salmon.

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 1. Egg and alevin	
1. Increased maintenance metabolism → smaller fry. 2. Lower disease resistance → lower survival. 3. Changed thermal regime during incubation → lower survival. 4. Faster embryonic development → earlier hatching–emergence. 5. More intense fall storms → redd scour and egg loss.	*Biological*: Developmental program is probably labile and fairly rapid selection for successful development under altered regime is possible, up to a point. *Management*: Cool water release from reservoirs upstream of spawners could ameliorate climate effects and (or) reduce scour. Protect spawning areas with cool groundwater discharge. *Policy*: Reserve flow of spawning rivers for fish to minimize thermal changes.
Stage 2. Fry: emergence to lake entry	
1. Faster yolk utilization → early emergence. 2. Smaller fry → lower survival rates. 3. Early emergence → mismatch with spring bloom. 4. Higher maintenance metabolism → greater food demand – slower growth – higher predation risk while foraging. 5. Smaller weaker fry → potential problems emerging.	*Biological*: Development program may adjust through selection so that emergence timing remains linked to zooplankton blooms. *Management*: Cool water release from reservoirs upstream of inlet spawners could ameliorate climate effects. *Policy*: Reserve flow of spawning rivers for fish to minimize thermal changes.
Stage 3. Fry: lake entry to first winter	
1. Warmer lake waters → higher maintenance metabolism → greater food demand – slower growth – higher predation risk while foraging. 2. Changing plankton phenology → disruption of lake food web – changed plankton community → poorer growth of fry. 3. Mismatch of lake entry to spring bloom → lower survival rate. 4. Earlier and stronger stratification → shallower thermocline → longer and stronger nutrient deficit in epilimnion during summer → lower plankton production → reduced food supply in midsummer → slower fry growth.	*Biological*: Fry may adjust vertical migration behaviour to take maximum advantage of energy saving in cool hypolimnion while foraging in epilimnion. Probable trade-off with predation risk because of the need to forage more in a warmer lake environment. *Management*: Fertilization of epilimnion during summer may mitigate effects of midsummer nutrient deficit. In smaller lakes, pneumatic mixing may help slow thermocline development. Enhanced harvest of predatory game fish may reduce predation pressure. *Policy*: Policies regarding predator management and bag limits for trout and other large fish may be revised to help keep predator populations low.
Stage 4. Fry: first winter	
1. Smaller size at start of winter → lower winter survival. 2. Warmer winter → higher metabolic demands → lower winter survival. 3. Warmer winter → increased predator activity – hunger → lower winter survival.	*Biological*: Winter has some of the greatest conflicting possibilities and unknowns. Situation will probably differ depending on lake type. *Management*: Take steps above to improve summer growth so fry enter winter at larger size. Take steps above to keep predator populations low. *Policy*: As above.

Table 1 (*continued*).

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 5. Smolting and seaward migration	
1. Smaller fry enter winter → smaller potential smolts → lower survival of smolts. 2. Smaller fry at end of first summer → delay of smolting 1 year → fewer smolts. 3. Earlier smolting → reduced marine survival. 4. Smaller smolts → poorer marine survival.	*Biological*: Timing of smolt migration is labile; population would probably adjust migration time fairly quickly. *Management*: Measures to ensure good fry growth above would also carry forward to winter survival and smolt size. *Policy*: If winter survival is mainly a matter of energy reserves, then there is probably not a policy response. If winter survival is predator driven, then policies affecting predator control apply here as well.
Stage 6. Postsmolts: estuary and coastal	
1. Smolt migration timing → timing mismatch with estuarine – nearshore productivity → lower growth–survival. 2. Altered coastal predator populations → greater mortality. 3. Altered prey populations → poorer growth → reduced survival during critical first summer. 4. Higher coastal water temperatures → greater maintenance metabolism → greater food demand → slower growth – lower survival. 5. Advection of acidified ocean waters onto continental shelf → impairment of shell-building plankton → poorer feeding for salmon. 6. Poorer growth in coastal waters → delayed transition to larger prey → poorer oceanic growth → smaller adult size.	*Biological*: Time of ocean entry, coastal migration tactics, predator avoidance tactics are labile behaviours, and in time fish might adapt somewhat, but it is doubtful that coastal habitats will be as productive for juvenile salmon under global warming. *Management*: Ensure minimum anthropogenic stressors during ocean entry phase (low tolerance for pollution, maintenance of physical habitats). *Policy*: "Salmon first" policy for estuarine and other critical nearshore habitats.
Stage 7. Immatures in the ocean	
1. Warmer surface temperatures → higher maintenance metabolism → higher food demand – slower growth. 2. Warmer temperatures → reduced suitable thermal habitat → greater competition for food → reduced growth. 3. Acidification of surface layer → lower plankton production → poor feeding conditions for salmon → reduced growth. 4. Changed structure and seasonality of forage organisms → changed foraging conditions → slower growth – higher predation risk.	*Biological*: Possible greater use of cool, deep water to offset higher metabolic rates in warmer surface waters and greater movement into the Bering Sea. However, these adaptations will also impose costs. *Management*: Ensure remaining high seas habitats are protected from fishing. Facilitate invasion of Arctic waters by salmon (by transplants or management of freshwater nurseries). *Policy*: Develop anticipatory policy to protect suitable salmon habitats in the Arctic and to facilitate the natural colonization that has already begun.

Table 1 (*concluded*).

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 8. Returning adults	
1. Reduced quality of marine nursery habitats → fewer and smaller adults with lower energy reserves returning to Fraser River → increased risk of en route and prespawning mortality. 2. Higher river temperature during upstream migration → greater energy cost – lower scope for activity during migration → higher risk of en route and prespawning mortality. 3. Higher temperatures during migration and spawning → greater risk of disease outbreak → greater risk of prespawning mortality. 4. Smaller adults → fewer smaller eggs → shorter development times, smaller fry, mistimed emergence. 5. Delayed maturation in ocean → lower marine survival → fewer adults returning.	*Biological*: Adaptive adjustments to ocean migration and maturation schedules are possible to improve potential for successful migration. Adaptive adjustments of optimal and critical temperatures for activity are also possible. *Management*: In the short term, rates of return, growth, etc. will be highly uncertain. Managers will need to reduce interception fisheries to ensure sufficient salmon reach spawning grounds. Commercial fisheries will need to be greatly reduced in capacity and perhaps eliminated altogether at some point. *Policy*: Reemphasize policy hierarchy of allocating salmon for spawning escapement first, then for aboriginal food and ceremonial purposes, before any commercial harvest. Make identification and protection of habitats that may still support salmon under global warming a policy priority.
Intergenerational effects	
Cumulative effects across life history stages and generations suggests the possibility of a downward spiral of size and productivity.	*Biological*: A multifaceted and uncertain set of adaptive responses is to be expected. Short-term adjustments will be within existing reaction norms. Longer term adjustments will involve genetic change. Overall capacity of the species to adjust is uncertain and will change as global warming proceeds. *Management*: Protect the species' opportunity to adjust and encourage it to invade new suitable habitats as they come available. *Policy*: Have a policy focus on maintaining and expanding the species' natural resilience.

Note: See appropriate text section on life history stages for more detail and references. Symbol "→" means "leads to". Note how effects at one stage affect performance at subsequent stages.

the Bering Sea, temperature may increase 3–7 °C (Mackas et al. 2007). There will be less precipitation as snow in the Fraser basin and more as rain. Coastal precipitation will increase but interior precipitation may decrease. Winter storm intensity will increase. Ocean surface waters will become less saline, stratification will intensify, and the thermocline may shoal. pH values low enough to affect calcification in marine organisms will rise into the surface layer in the North Pacific (Feely et al. 2008). The detailed effects of global change on freshwater and marine habitats of salmon remain very uncertain. However, current literature suggests the following.

Spawning streams during migration, spawning, and incubation

The majority of sockeye populations spawn in river systems that have a hydrograph dominated by snowmelt (a freshet in spring or early summer but with stable or declining flows during the late summer and winter spawning and incubation period; Mote et al. 2003). As climate warming proceeds, spring freshet will become earlier, smaller, and of shorter duration because of warmer temperatures and the decrease in seasonal snow pack (Morrison et al. 2002; Stewart et al. 2004). The rivers that sockeye use to access their spawning streams (e.g., Fraser, Thompson, Nechako) will be warmer and have lower discharge. Morrison et al. (2002) predict that by the end of the century, peak discharge in the Fraser River will decrease 18%, the peak will occur 26 days earlier (although in some years it may occur later because of heavy summer and fall rains), and the likelihood of migrating adult sockeye encountering temperatures greater than 20 °C will increase by a factor of ten. Spawning streams themselves will be warmer and discharge may be lower during the normal late summer – autumn spawning time and through the incubation period as permanent snow and glaciers disappear (Hauer et al. 1997; Melack et al. 1997). Not only will spawn-

ing streams be warmer on average but the schedule of temperature change during the incubation period may also change. Precipitation as rain rather than snow during late autumn and early winter may cause freshets large enough to scour spawning gravels (Melack et al. 1997; Stewart et al. 2004). Many spawning streams are ice-covered during winter months, and this ice cover will gradually disappear as winter temperatures increase. Coastal spawning streams will be warmer and may be subject to stronger winter freshets and greater scouring of spawning gravels as winter storms intensify (Melack et al. 1997). Temperatures in summer will be higher and base flows lower, particularly in smaller streams, which may cause stress for stream resident species like coho (*Oncorhynchus kisutch*) and Chinook but will be less important for sockeye (Mote et al. 2003; Ficke et al. 2007).

Nursery lakes

Sockeye nursery lakes in the interior of British Columbia are typically ice-covered or partially ice-covered during the winter. As global warming proceeds, these lakes will lose ice cover earlier in the year (or may not be ice-covered at all), will stratify thermally earlier and remain stratified longer, and will have higher summer epilimnion temperatures (Ficke et al. 2007). In interior lakes, nutrient depletion in surface waters will be more intense and last longer because of the strengthened and extended period of stratification (Henderson et al. 1992). Coastal nursery lakes will also stratify longer and have higher summer temperatures, but increased summer precipitation near the coast may moderate temperature increases somewhat and deliver nutrients to lake surface waters (Hauer et al. 1997; Melack et al. 1997).

Coastal marine habitats

Coastal waters of British Columbia will be warmer. In fact, coastal SST has increased about 1 °C over the past century (Roemmich and McGowan 1995; Mackas et al. 2007; Schwing et al. 2010). River discharge, which drives estuarine circulation, will be lower during spring freshet but higher during winter (and somewhat higher overall). The subarctic current system will move north so that more of southern British Columbia will be within the California Current system (Mackas et al. 2007). The spring transition from predominantly southeastern winds (which drive the poleward flowing, downwelling Davidson Current along the coast) to predominantly northwestern winds (which drive the equatorward flowing, upwelling California Current) will occur earlier in the spring (Mackas et al. 2007). Bakun (1990) suggested that alongshore winds may be stronger in summer, enhancing coastal upwelling, and there is some empirical support for this conjecture. However, modeling by Hsieh and Boer (1992) suggests that alongshore winds will be weaker and there will be a modest decrease in upwelling. McGowan et al. (1998) found that as the California Current has warmed over the second half of the 20th century, upwelling has drawn shallower, less nutrient-rich water to the surface. The Aleutian low will deepen and winter freshwater discharge from Alaska will increase so that the Alaskan gyre will speed up and buoyancy-driven flow along the coast of Alaska will be greater (Royer and Grosch 2006; Mackas et al. 2007; Schwing et al. 2010). Low pH waters will be drawn onto the coast by upwelling processes (Feely et al. 2008).

Gulf of Alaska

Climate variability in the North Pacific has been dominated by the Pacific Decadal Oscillation (Mantua et al. 1997), making it difficult to detect persistent trends in temperature; however, recent data show that the North Pacific has been warming for at least 60 years. Overland and Wang (2007) suggest that temperature increases due to anthropogenic climate change will exceed natural variation by about 2050, and temperature increases are expected to be 2–4 °C by the end of the century (Mackas et al. 2007; Barange and Perry 2009). Decadal variation will continue around the higher thermal mean. Salinity has also been declining in the North Pacific because of increasing precipitation over the ocean and coastal areas (Freeland et al. 1997). The precipitation increase over the ocean is expected to be about 100 mm·year^{-1} by the end of the century. Stratification has strengthened in the Gulf of Alaska and the thermocline has shoaled (Freeland et al. 1997). Upwelling of nutrients has declined at Station P (nitrate and silicate by about 25%), but concentrations are still greater than phytoplankton can utilize (production in the Gulf of Alaska is limited by iron) (Freeland et al. 1997; Mackas et al. 2007).

The surface layer in the North Pacific is expected to become sufficiently acidic to affect shell construction by plankton and benthos that build calcareous skeletons by mid-century (Fabry et al. 2008).

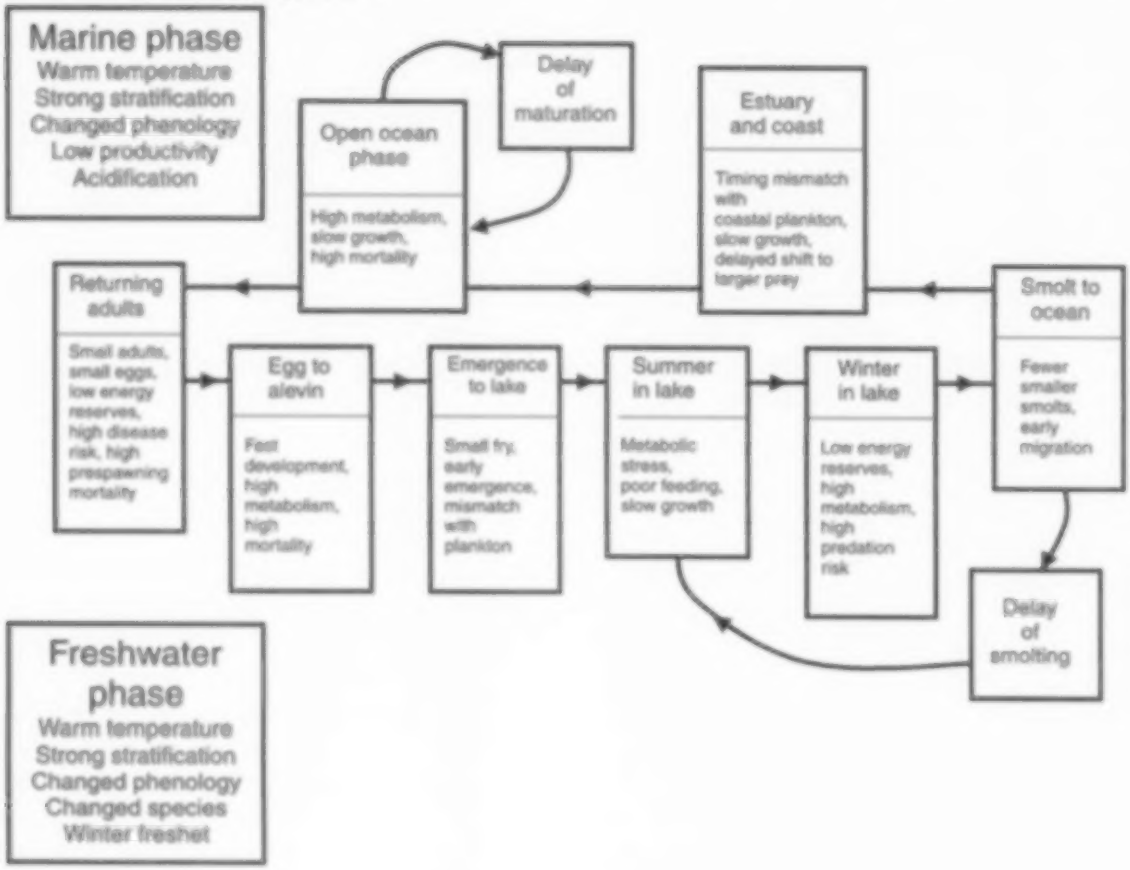
Responses of sockeye to changing freshwater and marine habitats

The responses of sockeye (and other species) to climate change will be complex and multifaceted. Freshwater and marine habitats will not all change in exactly the same ways or at the same times. For some populations and life stages, conditions may improve at first, while for others they deteriorate. Over time, however, all evidence points to a progressive decline in productive capacity of all stocks. Particularly important are the cumulative effects of change across life stages and habitats and across generations (Fig. 1; Table 1, columns 1 and 2). Below I provide details on life stage effects of climate change and their interstage and intergenerational consequences. Although specific counter examples to the general patterns I describe can certainly be found, the descriptions below represent, in my opinion, the most likely overall response of Fraser River sockeye (and other salmon species in the southern half of their geographic range) to climate change.

Stage 1. Egg and alevin

Embryonic development of sockeye eggs is temperature sensitive (Alderdice and Velsen 1978; Murray and McPhail 1988; Beacham and Murray 1990). Individual spawning populations appear to have specific development rate adaptations to conditions in their spawning stream (Tallman 1986; Beacham and Murray 1990). These adaptations ensure that sockeye fry emerge in the spring at the optimal time to take advantage of the spring zooplankton bloom in their nursery lake (Brannon 1987). Synchronized emergence from nearby spawning areas may also help swamp predator responses to fry, increasing survival probability (Tallman and Healey 1994). Under warmer incubation conditions, development

Fig. 1. Diagram of the conceptual model of the cumulative effects of climate change on Fraser River sockeye salmon. The diagram shows the eight life stages of sockeye salmon examined in the paper (boxes intersecting the life cycle loop), with freshwater stages below and marine stages above. Major effects of climate change are shown for each life stage. Major climate and ecosystem changes affecting salmon are shown in the boxes labeled "Freshwater phase" and "Marine phase". Salmon responses to climate change at one stage carry forward to affect performance at the next stage and between generations.



will be accelerated and the embryo will use more of its fixed store of yolk in maintenance metabolism. As a result, fry will be smaller and emergence timing will be earlier and may no longer coincide with development of the fry's food supply (Walther et al. 2002; Winder and Schindler 2004*a*). As discussed later, cumulative effects of climate change are likely to lead to smaller adults that will produce smaller eggs, which develop more quickly, exacerbating any problems of small size and early emergence of fry. Small eggs have also been shown to have reduced survival compared with large eggs in brown trout (*Salmo trutta*) and Chinook salmon (Bagenal 1969; Heath et al. 1999). Other studies, however, have not found a similar relationship (Beacham and Murray 1985; Hutchings 1991). Eggs subject to altered thermal regimes during development may also suffer high mortality (Tallman 1986).

Fall rainstorms (that previously would have fallen as snow) may scour embryos from spawning nests (Cunjak et al. 1998; Steen and Quinn 1999). Montgomery et al. (1996) suggest that even a small increase in scour depth could have a big impact on embryo survival. Smaller adults resulting from global warming (see later discussion of marine growth) will construct shallower redds, increasing the probability of scour (Steen and Quinn 1999). Autumn storms are also likely to be more intense, increasing the probability of scour. Because of more variable fall and winter discharge, sockeye may spawn in marginal areas that dry up when water levels fall. Changes in winter temperatures can affect the likelihood that frazil or anchor ice will form in spawning beds that can penetrate redds and freeze or smother embryos (Reiser and Wesche 1979; Cunjak and Therrien 1998). In the long term, the mortality risk from this factor will go down, but as very cold winters warm up, the risk will at first increase as areas of open water encourage the formation of frazil ice (Bisaillon et al. 2007).

In summary, incubation at higher temperatures and under more variable flow regimes is likely to result in fewer, smaller fry surviving to the time of emergence. Fry will also reach the emergence stage earlier, a change in phenology that may be maladaptive (Fig. 1; Table 1).

Stage 2. Fry: emergence to lake entry

Emergence from the gravel spawning nest can be a difficult time for salmon fry, particularly if sediment plugs gravel during incubation (Phillips et al. 1975; Mackenzie and Moring 1988; Pauwels and Haines 1994). Autumn storms falling as rain rather than snow have the potential to wash fine sediments into spawning streams, partially plugging interstitial spaces and making fry emergence more difficult. Any factors that reduce fry competence, such as reduced energy reserves or incomplete development, are likely to increase mortality at this time. Predators also cue onto emerging fry so that smaller fry with reduced swimming competence will be subject to higher predation risk (Taylor and McPhail 1985).

Once fry emerge from the gravel nest, they migrate to a nursery lake. When the nursery is downstream from the spawning location, fry need only drift to the lake. However, when the nursery lake is upstream, fry must migrate against the current. Smaller fry may be less able to make such an upstream migration successfully (Taylor and McPhail 1985). Patterson et al. (2004) found that sockeye spawning in outlet streams had larger eggs and produced larger fry that had greater swimming capability than sockeye spawning in inlet streams. This suggests that the smaller fry expected under global warming will find it more difficult to reach their nursery lake. Smaller fry may also expend more energy to reach the nursery lake, particularly if the water is warmer, so that their need for abundant food may be even greater than under present circumstances. This difficulty may be somewhat mitigated if spring discharge is reduced so that the velocities fry encounter are lower

Once in the nursery lake, fry feed and grow on limnetic zooplankton. Under natural conditions, fry entry into the nursery lake is timed to coincide with the spring bloom of lake zooplankton (Brannon 1987). Changes in the phenology of fry emergence may mean that the time of lake entry no longer coincides with the spring zooplankton bloom. Changes in phenology of phytoplankton and zooplankton in the nursery lake could accentuate this problem. Changes in phenology leading to mismatch between predators and prey are a frequently observed consequence of climate change (Parmesan and Yohe 2003; Edwards and Richardson 2004; Hays et al. 2005). Winder and Schindler (2004*a*, 2004*b*) have shown that as Lake Washington has become warmer, the spring bloom of zooplankton has become uncoupled from the spring phytoplankton bloom, resulting in lower spring zooplankton densities and poorer feeding conditions for sockeye fry. As warming continues, zooplankton composition in Lake Washington may also change from large *Daphnia* to smaller *Bosmina* and copepods, providing a less valuable food for sockeye fry.

Hutchings (1991) found that size and survival of brook trout (*Salvelinus fontinalis*) fry was positively correlated with egg size over the first 50 days after emergence regardless of feeding conditions. Under reduced feeding conditions, however, fry from smaller eggs had much higher mortality, whereas mortality of fry from larger eggs did not change. If similar relationships exist for sockeye, any reduction in egg size and (or) mismatch between fry emergence and food production could dramatically reduce survival from emergence to lake entry, particularly in outlet spawning populations.

In summary, the smaller fry that result from smaller eggs and warmer incubation conditions are expected to experience higher mortality from a number of factors, such as problems emerging from gravel nests, poorer swimming competence and greater vulnerability to predation, timing mismatch between fry emergence and spring zooplankton production, and changes in lake zooplankton that reduce its value as food for sockeye fry. As a consequence, fewer fry will make it into the nursery lake and their growth rate during the critical first feeding stage will be slower (Fig. 1; Table 1).

Stage 3. Fry: lake entry to first winter

Sockeye fry feed on pelagic zooplankton throughout their year or so of lake residence. Hampton et al. (2006) have shown that *Daphnia* population growth in Lake Washington has become less concordant with sockeye fry arrival. In addition, sockeye's preferred forage species, *Daphnia pulicaria*, has become relatively less abundant compared with the less preferred *Daphnia thorata*. The longer open water season in lakes under global warming will potentially provide for a longer growing season. However, as long as the lake remains stratified, nutrient concentrations and plankton production in the surface waters will be low, offering a limited feeding and growth opportunity for sockeye. The duration of stratification in Lake Washington has increased by about 4 weeks since 1962 (Winder et al. 2009). Surface waters will also be warmer, increasing energy costs and disease risk for sockeye fry. In Lake Washington, temperature of the epilimnion has increased by about 1.5 °C since 1962 (current maximum epilimnion temperatures are 18–20 °C; Arhonditsis et al. 2004). Henderson et al. (1992) suggest that in Shuswap Lake, a major sockeye nursery lake in the Fraser basin, surface temperatures in midsummer may exceed 26 °C within a few decades, lethal to young sockeye if they spend more than a few minutes above the thermocline (in 1999, epilimnion temperature was 25 °C). Not all Fraser basin nursery lakes have such high epilimnion temperatures, however. Chilko Lake, for example, seldom has epilimnion temperatures above 14 °C (Hume et al. 1996). In many nursery lakes, sockeye fry undertake daily vertical migrations to avoid warm temperatures and predators in the surface waters for much of the day. Under global warming, their vertical excursions into the surface waters to get food during dawn and dusk may have to be shortened, and the higher average temperature they experience will increase metabolic costs. Henderson et al. (1992) conclude that growth of sockeye in Shuswap Lake during their first summer will be reduced under global warming. This is likely also to be the case in many other nursery lakes in the Fraser River drainage.

West and Larkin (1987) found that growth of sockeye fry in Babine Lake was size-dependent, with smaller fry growing more slowly. The smaller fry produced under global warming may, therefore, already be at a growth disadvantage regardless of any phenological mismatch between fry and their zooplankton prey or changes in zooplankton community composition. The literature generally indicates that mortality of salmon fry in freshwater nursery habitats is size-dependent, with smaller fry suffering higher mortality (West and Larkin 1987; Sogard 1997; Einum and Fleming 2000), although under some circumstances larger fry can suffer higher mortality (Holtby and Healey 1986; Good et al. 2001).

Under global warming, therefore, Fraser River sockeye fry are likely to be smaller on average at the end of their first summer. Small size (as emergent fry facing poor growing conditions in the lake) may cause the fry to adopt risky foraging behaviour that exposes them to thermal stress, greater predation, and greater risk of disease (Eggers 1978). West and Larkin (1987) found that size-selective mortality was strongest during the late summer and autumn in Babine Lake. This may indicate that the smaller fry were risking predation to build their energy reserves sufficiently to survive the winter fasting period (see next section). It seems likely, therefore, that under global warming, fry growth during the first summer will be lower and mortality rates higher than normal. As a consequence, fewer, smaller fry will enter the winter with, on average, lower energy reserves (Fig. 1; Table 1).

Stage 4. Fry: first winter

The first winter is considered a critical time for young salmon and is often a time of high mortality (Bisaillon et al. 2007; Jonsson and Jonsson 2009). Overwinter mortality is negatively correlated with size and body energy reserves (Sogard 1997; Biro et al. 2004; Finstad et al. 2004), so smaller, more poorly fed fry entering the winter are likely to suffer high mortality. Factors associated with winter mortality include predation, energy exhaustion, and susceptibility to extreme conditions of flow and temperature; small fry are more vulnerable to all these factors. Crozier and Zabel (2006) found that survival for Chinook salmon in 18 streams in the Salmon River basin, Idaho, was positively associated with autumn discharge, although for some populations a negative relationship with summer temperature was stronger. Cunjack et al. (1998) found that winter survival of all life stages of Atlantic salmon (*Salmo salar*) in Catamaran Brook, Newfoundland, was positively associated with winter discharge. Most data on winter survival refer to stream-dwelling salmonids, and lake-dwelling sockeye may be less susceptible during this period. Predation and energy exhaustion are likely to be the most important factors for overwinter survival of sockeye.

In summary, as global warming proceeds, sockeye fry will enter the winter at smaller size and with lower body energy reserves and will suffer greater than normal overwinter mortality. Thus, fewer fry will make up the pool of potential smolts in spring, and these fish are likely to be in poor condition (Fig. 1; Table 1).

Stage 5. Smolting and seaward migration

Smolt transformation is a critical life history stage in anadromous salmon, involving physiological and behavioural changes that allow the fish to survive in seawater (Folmar and Dickhoff 1980; McCormick et al. 1998). Salmon fry must have achieved an appropriate size and development stage to undergo successful smolting. The majority of Fraser River sockeye smolt at 1 year of age, although some smolt at 2 years of age. It appears that the decision to smolt is made well before smolting occurs, probably during the summer growth phase (Thorpe et al. 1992; Hinch et al. 2006), and is connected with growth rate. The probability that an individual fish will smolt is positively correlated with the size at which it enters the winter, and there is evidence of a minimum size for successful smolting (Folmar and Dickhoff 1980). The physiological and behavioural characteristics related to smolting develop in the early spring, rise to a maximum, and then fade away if the fish does not initiate seaward migration. Furthermore, the physiological "time window" during which successful smolting is possible is shorter under warmer conditions (McCormick et al. 1998). Smaller parr may move through this window before reaching full competence to smolt, thus forcing a 1-year delay of smolting. Fry that grow more slowly under global warming, therefore, may spend a second year in fresh water before going to sea. Or, they may decide to smolt at small size. Small fish that proceed to smolting typically show rapid growth in the spring prior to seaward migration, which brings their size closer to that of larger smolts (Eggers 1978; Nicieza and Branya 1993). Sockeye that delay smolting face a second year of mortality in the lake and increase their generation time by 1 year, both of which reduce overall productivity. Sockeye that decide to smolt at small size and feed to grow rapidly in early spring face elevated mortality risk. Davidsen et al. (2009) observed that small Atlantic salmon smolts had low survival over 11 km of river migration, and numerous authors have shown a relationship between smolt size and overall marine survival for sockeye salmon (Henderson and Cass 1991; Koenings et al. 1993).

The timing of smolt migration is cued by photoperiod but is triggered by temperature, advancing several days under warm conditions and delaying under cold conditions in the spring (McCormick et al. 1998; Jonsson and Jonsson 2009). Therefore, warmer spring temperatures may advance the smolting date. However, smaller fish also migrate somewhat later and will also be trying to put on as much spring growth as possible before migrating to sea, so that the influence of temperature on smolting phenology may not be as large as if the presmolts were of normal size (Nicieza and Branya 1993; Beckman et al. 1998). However, even small changes in migration timing can increase mortality risk (Bilton et al. 1982; McCormick et al. 1998), as there appears to be an optimal environmental window for successful smolt migration as well as an optimal physiological window. It seems unlikely that changes in smolt migration timing will match phenological shifts in estuarine and coastal ecosystems in such a way that marine growth and survival are not affected.

In summary, under global warming, yearling sockeye smolts will migrate somewhat earlier and at smaller size. More fry will delay smolting until their second year. Fewer, smaller smolts will enter the ocean, and their timing is likely to be mismatched with ocean feeding and growth opportunity (Fig. 1; Table 1).

Stage 6. Postsmolts: estuary and coastal

Several authors have presented evidence that survival during the first months of marine life is critical to the abundance of returning adult salmon (e.g., Holtby et al. 1990; Friedland et al. 2000; Mueter et al. 2005). Overall marine survival is strongly related to the size of smolts entering the sea and (or) early marine growth rates (Holtby et al. 1990; Koenings et al. 1993; Friedland et al. 2000). As Mangel (1994) pointed out, growth at this stage is crucial because salmon avoid predation by growing larger than predators can easily capture. Conditions for growth of Fraser River sockeye during the

first months of marine life are, therefore, critical to overall marine survival and productivity.

Sockeye smolts from Fraser River stocks typically begin arriving in the Strait of Georgia in the latter half of April, and the migration continues through May (Groot and Cooke 1987; Tucker et al. 2009). Initially, postsmolts are concentrated in the area of the Fraser River plume but then migrate north through the Strait of Georgia, Johnstone Strait, and Queen Charlotte Strait, reaching Queen Charlotte Sound in late June or July (Groot and Cooke 1987; Tucker et al. 2009). The details of their movement beyond this point are unknown, but they continue to move north and west in continental shelf waters until sometime in the autumn when they move offshore into the Gulf of Alaska (Walter et al. 1997; Healey 2000; Tucker et al. 2009).

The precise changes in environment and feeding conditions in the coastal ocean under global warming are uncertain, but as noted earlier, coastal waters will be warmer, the spring transition to upwelling conditions on the south coast of British Columbia will be earlier, and spring freshet from the Fraser River will be lower, reducing estuarine circulation and productivity in the Strait of Georgia (Yin et al. 1997*a*, 1997*b*; Mackas et al. 2007). Mackas and Louttit (1988) showed that the copepod *Neocalanus plumchrus* (and probably other zooplankton and small fishes as well) was concentrated in the advancing plume of the Fraser River, which may enhance feeding opportunity for sockeye smolts in the estuary (Healey 1980). *Neocalanus plumchris* is the dominant spring zooplankter in the Strait of Georgia, with an intense but short-lived peak in abundance. The timing of the *N. plumchrus* peak is responsive to temperature in the mixed layer and advances during warm years (Mackas et al. 1998). The timing of the peak at the end of the 1990s (April) was almost a month earlier than in the 1960s (May), probably due to the increase in mixed layer temperature over that period (Bornhold 2000). This degree of phenological change in the zooplankton of the Strait of Georgia is much greater than any as yet observed change in salmon smolt timing, so that even with an advance in the timing of smolt migration, there may be a big mismatch between the timing of sockeye arrival in the Strait of Georgia and the abundance of this large and dominant copepod.

Neocalanus plumchrus is, at best, a short-term forage species for Fraser River sockeye in coastal waters, and in recent years its peak abundance has become even shorter (Batten and Mackas 2009). By the time sockeye are migrating north out of the Strait of Georgia, *N. plumchris* is returning to deep water. Coastal zooplankton are, however, the dominant food of sockeye during their period of residence in continental shelf waters (Brodeur 1990). Under warming conditions, the subarctic front is pushed northward at least to Haida Gwaii, and the plankton community off British Columbia comes to resemble that of the California Current with abundant small copepods but low biomass (Fulton and LeBrasseur 1985; Mackas et al. 2001, 2007). Under these conditions, salmon and other predators show poor survival and growth (Gaston and Smith 2001; Mackas et al. 2007). Mackas et al. (2007) described this as the "warm, unproductive" community. Presumably, under global warming, these conditions will become permanent or semipermanent off the British Columbia coast, reducing the growth and survival of young salmon.

Other changes in the coastal ocean associated with global warming will also affect growth and survival of salmon. The biological community of the Gulf of Alaska changes with changing ocean conditions, and the suite of predators that salmon will face is expected to change as marine species adjust their distributions to increasing SST (Karinen et al. 1985; see also Appendix 1 in Fulton and LeBrasseur 1985; Anderson and Piatt 1999). In addition to facing a changing predator community and reduced food supplies, foraging opportunity may be further changed by ocean acidification (Fabry et al. 2008; Feely et al. 2008). Pteropod mollusks, an important food of young salmon during the first summer, may be adversely affected by declining pH, which makes it difficult for them to construct their shells. Aydin et al. (2005) showed that this rich food source was critical for young pink salmon, allowing them to grow rapidly during early marine life and make the transition to feeding on squid. Final adult size in pink salmon was very sensitive to the timing of this ontogenetic shift in diet. Beauchamp et al. (2007) determined that higher survival of pink salmon in the Gulf of Alaska was associated with high foraging on pteropod mollusks during July–August of the first year of ocean life. In addition, phenological changes in the trophic web supporting young salmon and in the timing of salmon migrations themselves seem likely to degrade further the quality of the coastal environment as a nursery for young salmon (Edwards and Richardson 2004; Mackas et al. 2007).

In summary, the coastal ocean under global warming will change in ways that are not favourable for Fraser River sockeye and other salmon species from the region. There is a growing body of evidence that larger size at ocean entry and rapid early marine growth lead to high adult abundance and large adult size. A warmer coastal ocean supports a zooplankton community that is less valuable as food for young Fraser River salmon and an altered community of predators to which young salmon are less well adapted. In addition, an increasingly acidic ocean will affect production of important forage species such as pteropod mollusks that young sockeye should encounter as they migrate north along the coast. Couple these changes with changes in phenology of both salmon and food and the result is likely to be a coastal ocean ecosystem that is much less supportive of young salmon. As a result, the smaller smolts produced from the freshwater nurseries of the Fraser River will grow more slowly and experience higher mortality during their time in coastal marine waters (Fig. 1; Table 1).

Stage 7. Immatures in the ocean

After they leave coastal waters, the Gulf of Alaska is the primary feeding area for Fraser sockeye. Although sockeye movement patterns in the ocean are not well understood, they are probably moving so as to maximize their growth potential in a relatively unproductive environment (Healey 2000; Rand 2002). Global warming is likely to make this nursery warmer and less productive than in the past, although the degree of change is uncertain (Hinch et al. 1995*b*; Falkowski et al. 1998; Pierce 2004). All salmon species, and Fraser River sockeye in particular, are returning at smaller adult size (within age classes) compared with a few decades ago (Bigler et al. 1996; Cox and Hinch 1997), and these changes can be linked to warmer temperature in the Gulf of

Alaska but also to salmon density and estimates of food supply (Hinch et al. 1995*a*, 1995*b*; Cox and Hinch 1997). Returning sockeye are also older on average (Pyper et al. 1999; Morita et al. 2005), suggesting that reduced marine growth rates have caused some salmon to delay maturation. Delay of maturation will mitigate the declining size at age to some degree, but delayed maturation also means additional mortality at sea and a lengthened generation time, both of which will contribute to reduced productivity.

Welch et al. (1998) described sharp thermal limits for sockeye in the North Pacific and showed that under global warming, suitable thermal habitat for sockeye may disappear from the North Pacific. Sockeye may avoid higher temperatures in surface waters of the Gulf of Alaska by spending more time below the mixed layer or retreating north to remain within their thermal habitat preferences (Welch et al. 1998). Rand (2002) argued that salmon thermal preferences represent selection of thermal habitats where positive growth is possible rather than a response to temperature per se, as all temperatures were well within the species' tolerance. Nagasawa (2000) analyzed the winter biomass of zooplankton in the North Pacific and the distribution of salmon. Plankton biomass in winter was <10% of summer biomass, and in winter salmon were found predominantly in temperatures <8 °C. He argued that selection of low temperatures was a tactic for minimizing metabolic losses when feeding opportunity was low. Redistributing to the north and into the Bering Sea as the ocean warms will expose sockeye to higher densities of competitors, further reducing foraging efficiency. For Fraser River sockeye, such redistribution will also commit them to a much longer return migration through a warm and unproductive region of ocean at a time when they should be growing rapidly (Brett 1983).

There are many gaps in the data on ecosystem-level effects of climate on salmon in the North Pacific. The picture for Atlantic salmon in the North Atlantic is somewhat clearer. In the eastern Atlantic, Beaugrand and Reid (2003) have shown that SST has increased in recent decades, and phytoplankton productivity and the abundance of small copepods has also increased. The abundance of large copepods (e.g., *Calanus finmarchicus*) and Atlantic salmon, however, has decreased, suggesting a breakdown in the food chain supporting salmon. Edwards and Richardson (2004) have also shown divergent phenological responses among the phytoplankton, zooplankton, and zooplankton predators in the North Sea, resulting in considerable disruption of the trophic structure. In the Atlantic as in the Pacific, global warming is linked to declines in salmon production.

There are other emerging problems. As with coastal waters, oceanic waters are subject to acidification from the absorption of excess CO_2. Orr et al. (2005) provide data and models to suggest that pH low enough to cause decalcification in various phytoplankton and some zooplankton that are food for salmon could occur in high latitude surface waters before the end of the century. Salmon may escape some aspects of changing ocean conditions (such as unfavourable temperatures) by changing their distribution. However, the effects of acidification are likely to be pervasive.

In summary, overall productivity of the North Pacific food web supporting salmon may decline under global warming; it seems unlikely to increase. As in the Atlantic, diverse phenological responses among the plankton and other forage species are likely to disrupt the food web supporting salmon. The subarctic front in the North Pacific, which is usually the southern boundary of sockeye distribution, will shift north, reducing habitat area. Suitable thermal habitats may even contract into the Bering Sea, driving up competition among salmon and further reducing growth. The marine phase of homeward migration for maturing Fraser River sockeye will be longer and through relatively warm, unproductive waters, further restricting growth at a time when the fish typically accumulate up to 30% of their mature biomass (Brett 1983; Hinch et al. 1995*a*, 1995*b*). In keeping with empirical trends that have already been observed, as the North Pacific continues to warm, Fraser River sockeye will return at smaller size and older average age and there will be fewer of them (Fig. 1; Table 1).

Stage 8. Returning adults

Sockeye typically mature at a number of different ocean ages, although 4-year-old fish (age 1.2, one freshwater winter and two ocean winters) are by far the most abundant in the Fraser River (Foerster 1968; Healey 1986). We can assume that a salmon must reach an appropriate size and development stage in the spring if it is to initiate maturation and homeward migration. There is, presumably, a critical size threshold and perhaps a critical growth rate threshold that triggers the maturation–migration process. Once maturation is initiated, sockeye undertake a directed migration back to their river and upstream to their natal spawning ground (Healey and Groot 1987; Burgner 1991). Genetics, maternal effects, and environment all affect the age at which a salmon matures (Bradford and Peterman 1987; Heath et al. 1994; Wood and Foote 1996). The decline in size of mature sockeye returning to the Fraser River, together with their increase in average age, suggests that some fish are reaching a sufficient size to trigger homeward migration at the usual age but others are opting to delay maturation. Not only are sockeye returning at smaller size in recent years but they also appear to be returning at lower body energy density (Crossin et al. 2004*a*). Energy reserves at time of river entry are critical, as salmon do not feed in fresh water and must complete their migration, complete maturation, and spawn using these reserves. Most sockeye returning to the Fraser River must undertake an arduous upstream migration of many hundreds of kilometres before reaching their spawning streams (Healey et al. 2000). Mortality occurs when sockeye reach a body energy density of about 4 $MJ \cdot kg^{-1}$, so that fish must complete their migration and spawning before reaching this threshold (Crossin et al. 2004*b*). In recent years, some sockeye populations have been returning to the Fraser River weeks earlier than in the past, and a high proportion has died en route to the spawning grounds (Cooke et al. 2004). Others have reached the spawning grounds but died without spawning. Energetic exhaustion is one likely explanation for at least some of this mortality, although there is, as yet, little direct evidence of en route or prespawning mortality due to energy exhaustion (Rand et al. 2006). Temperature, stress, and disease are also implicated (Cooke et al. 2004; Farrell et al. 2008; Martins et al. 2011).

Problems with "missing" sockeye in the Fraser River and the unprecedented early return and high mortality of some

stocks during the past decade (Cooke et al. 2004; Williams 2005) has stimulated considerable research on the physiology and behaviour of salmon during upriver migration (e.g., Hinch and Rand 1998; Lee et al. 2003; Crossin et al. 2009). Although the precise causes of early return to the river and mortality prior to spawning remain unclear, much of this research is relevant to the potential effects of climate change on Fraser River sockeye, in particular the findings regarding temperature adaptation (Farrell et al. 2008). Fraser River sockeye from different spawning populations return to the river at various times throughout the summer, when river temperatures are near their seasonal maximum. Individual salmon populations show adaptations such that the temperature (T_{opt}) of their maximum scope for activity is the temperature they would normally encounter during their upstream migration. However, scope for activity falls off sharply at temperatures above this optimum so that the critical temperature (T_{crit}), at which there is effectively no scope for activity, is only 6–7 °C higher than T_{opt}. In very warm years, such as 2004, migration can be stalled and high en route or prespawning mortality can occur because temperatures approach T_{crit} (Williams 2005; Farrell et al. 2008). One experiment with Weaver Creek sockeye showed that sockeye exposed to 18 °C (about 4 °C above T_{opt} for this population) for 24 days and released back into the river suffered higher mortality and showed greater expression of the parasite *Parvicapsula minibicornis* than a second group exposed for the same period to 10 °C or an untreated control group (Crossin et al. 2008). The narrow temperature spread between T_{opt} and T_{crit} means that even a modest increase in river temperatures can compromise migration and reproductive success, especially in fish that may be experiencing other stressors.

Maximum summer temperatures in the Fraser River have increased by an average of 1.8 °C since 1950; whereas these temperatures used to range from 16 to 20 °C, they now range from 18 to 22 °C (Patterson et al. 2007; Farrell et al. 2008). Hyatt et al. (2003) suggested that 21 °C was a critical temperature for migration of Okanagan River sockeye: migration stopping as temperature rose above 21 °C and resuming when temperature fell below 21 °C. Presumably, the critical temperature blocking migration will differ according to the temperature adaptation of the salmon population. The experiment of Crossin et al. (2008) indicates that exposure even to relatively moderate temperatures can have a serious effect on migration success. The 1.8 °C increase already observed in maximum river temperatures means that migration capacity of sockeye may already have been reduced by an average of 25%. Coupled with the greater metabolic costs and risk of disease that come with higher temperatures, it is perhaps not surprising that Fraser River sockeye have been experiencing high en route and prespawning mortality, especially in warm years.

Fish that die without spawning are completely lost in terms of contributions to the next generation. However, smaller females also lay fewer, smaller eggs, so that even the fish that spawn make a lower per individual contribution to the next generation (Healey 1987).

In summary, under global warming sockeye will return to the Fraser River at smaller size and with lower body energy reserves, which may compromise their ability to complete migration and spawning. In addition, higher temperatures during upstream migration may cause migration delays or stop migration altogether. Stressed fish in the warmer river will be subject to greater risk of disease. High mortality during upstream migration and prior to spawning is the likely result. Those fish that do spawn will lay fewer and smaller eggs, thus compromising productivity of the next generation (Fig. 1; Table 1).

Synthesis — cumulative effects

Any forecast of the effects of climate change has high uncertainty; however, the evidence presented above shows that global warming will likely have negative effects on productivity of Fraser River sockeye at every life history stage. Although not all environmental and ecological change with global warming will be negative for Fraser River sockeye (warmer temperatures will enhance lake and ocean productivity in some regions, for example, and lower spring and summer discharge may make upstream migration easier), the weight of evidence supports the conclusion that effects at each stage will be predominantly negative. Furthermore, the effects at one stage carry forward to the next.

The cumulative effects model can be described as follows in relation to historic norms (see also Fig. 1; Table 1): (1) Warmer incubation temperatures will result in fewer, smaller fry emerging from the gravel nests. More variable autumn and winter flows may also result in substantial scour of spawning nests. Fry from outlet spawning beds will have more difficulty reaching the nursery lake. Overall, fewer and smaller fry will enter the nursery lake earlier in spring. (2) Smaller fry will enter a warmer nursery lake where phenological changes in plankton communities have disrupted trophic relationships. As a consequence, fry will grow more slowly in the lake and will experience higher mortality. (3) Fry will enter the critical first winter at smaller size with lower energy reserves and will experience higher mortality as a result. (4) Fewer fry will have achieved the size – life stage threshold to smolt after 1 year so that a higher percentage of fry will delay smolting, experiencing a second year of freshwater mortality. Fry that do smolt after 1 year will be smaller than normal. Overall, fewer, smaller smolts will be produced from the nursery lake, and they are likely to migrate somewhat earlier. (5) Smolts will enter a warmer, less productive coastal ocean where trophic relationships have been disrupted by phenological changes that will likely not match the phenological change in smolt migration timing. Dominant zooplankton in the warmer ocean will be less suitable as prey for salmon. As a result, postsmolt growth will be slower, further compromising an already low survival rate because of their small size at ocean entry. Ocean acidification may also compromise the abundance of important prey such as pteropod mollusks. Ontological transition to feeding on larger, energy-rich prey, like squid, will be delayed. (6) Poor growth in coastal waters will carry forward into the oceanic phase. Suitable thermal habitats in the North Pacific will be pushed north by global warming so that fish will be concentrated into a smaller area of ocean and feeding competition will be greater. As a result, fish will be smaller at their normal maturation age, and a higher proportion of any year class will delay maturation by an extra year. Fewer, smaller adults will make the spawning migration each year. (7) Smaller adults

will return to the river mouth with lower body energy density, perhaps insufficient for them to complete the spawning migration and spawn in a warmer river. Upriver migration may be delayed because of reduced scope for activity in the warmer river. Mortality during upriver migration will be higher so that fewer, smaller adults arrive at the spawning grounds. (8) Smaller females with lower energy reserves will have lower capacity to construct and defend a redd so that egg burial depth will be lower and potential for superimposition higher. Eggs that are buried at shallower depth will be at greater risk of scour during autumn storms. Smaller females will also lay smaller eggs, so that development will be further accelerated in the subsequent generation, increasing the phenological change in fry emergence timing. (9) Compensatory delays in smolting and maturation will extend generation time, further reducing overall productivity. (10) Finally, as suggested in point 8 above, effects in one generation will carry forward to the next generation, potentially creating a downward spiral in size, survival, and productivity in each generation.

Though qualitative, this model is well supported by the literature, and a quantitative evaluation of salmon responses to climate change would clarify the relative importance of change at different life stages and show how change would propagate through the life cycle and across generations. Quantitative modeling would also reveal which parameters are most in need of further research. A team of researchers from Washington State and British Columbia has begun developing a model that will be a critical step toward this objective (Mantua et al. 2009).

If global warming can be stopped before a critical stage is reached, the Fraser River system will eventually settle into a new regime of production. However, on the basis of present evidence, it seems doubtful that the new regime would involve substantial commercial production of salmon. Indeed, it seems more likely that many Fraser River sockeye populations will be extirpated, and those that remain will be in a tenuous position. One critical stage would be when maximum river temperatures regularly reach T_{crit} for most populations. However, it is unlikely that temperatures would have to rise even to this level before salmon populations suffered physiological collapse (Farrell et al. 2008).

Although I developed the conceptual model for Fraser River sockeye, its main elements can easily be extrapolated to the other anadromous Pacific salmon species. All species will experience adverse changes in incubation and freshwater nursery environments in the southern portions of their ranges (higher temperature, redd scour). All species will experience coastal and oceanic environments that are warmer and reduced in productivity with changed predator species. It seems likely that by 2050 the majority of freshwater and marine habitats of Pacific salmon from the central British Columbia coast south to the limit of salmon distribution will become much less hospitable to salmon, and production in this region will be dramatically reduced. Populations in northern British Columbia and Alaska (and Russia), however, should experience improved productivity, at least for a while (see e.g., Edmundson and Mazumder 2001; Mueter et al. 2002; Schindler et al. 2005). Indeed, salmon catches in eastern Russia and Alaska are currently at all-time highs, partly because of increased hatchery production of chum (*Oncorhynchus keta*) and pink (*Oncorhynchus gorbuscha*) salmon (Irvine et al. 2009*a*; Nagasawa and Azumaya 2009). Pink and chum salmon are also currently abundant in the southern part of their range (Irvine et al. 2009*a*). However, as global warming continues, these populations will eventually begin suffering overall negative effects, first in the south but progressing northward with time.

Mitigation and adaptation

Mitigating the effects of global warming on salmon is difficult, and it is unlikely that any mitigation will sustain salmon populations in the long run as global warming continues. However, there are some policies and practices that would slow rates of decline and help ensure continued survival of at least some southern salmon populations. The wild salmon policy (Fisheries and Oceans Canada 2005; Irvine 2009) provides a solid foundation for conservation and sustainable use under historic patterns of environmental variation. Some policy and management options for minimizing the impact of climate change are summarized (Table 1, column 3; see Nelitz et al. 2007, 2010, for a detailed discussion of policy and management options related to specific habitats and populations as well as for a conceptual model of the effects of climate change similar to the one presented here). All of these policies and practices involve foregoing other options. They also require a dramatic change in the focus of policy and management, changes that have already begun under the wild salmon policy.

To some extent, biological responses of the fish themselves will help to mitigate the effects of climate change (Table 1). Many life history characteristics have a fairly broad reaction norm, and genetic change can occur quite quickly in some instances. Crozier et al. (2008) discussed the capacity of Chinook salmon to respond phenotypically and genotypically to aspects of climate change in some detail. Presumably, other species will have similar capacity for evolutionary response. Predicting the overall pattern of change is difficult because, as Crozier et al. (2008) point out, changes at one stage can have repercussions for later stages, particularly when life stage transitions are finely tuned to conditions in radically different environments. Based on Crozier et al. (2008), traits with the greatest likelihood of an evolutionary response to climate change include heat tolerance (and perhaps T_{opt} and T_{crit}, see earlier), disease resistance, metabolic efficiency, migration timing, and spawning date. Unfortunately, it is doubtful that phenotypic or evolutionary change in these characters will be sufficient to prevent the expected decline in productivity.

Policy and management changes can also help mitigate the impacts of climate change; however, their focus must change from maximizing the potential commercial harvest to maximizing salmon resilience (Healey 2009). The wild salmon policy mandates these kinds of changes. Changes in freshwater habitats will not be uniform, and some habitats will retain capacity to support salmon much better than others. Habitats that will retain favourable characteristics longest under global warming need to be identified and conservation should target those habitats. On tributaries with reservoirs, reservoir operation to favour salmon conservation and release of deep water to cool downstream habitats should become a

priority. It may even be worth considering construction of reservoirs to provide water storage and cool water to help sustain particularly valuable stocks. Regardless, a stronger policy of reserving river flow for salmon conservation will have to be adopted. As temperatures warm, reducing other forms of anthropogenic stress on salmon will become even more important. As not everything can be protected, hard choices will need to be made about where conservation should occur. Conservation should focus on the habitats and stocks most likely to survive under global warming rather than on those where the trade-offs are easiest. For fuller discussion of these and other policy and management options, see Nelitz et al. (2007, 2010).

The most positive opportunities for sustaining salmon appear to be in the far north, where the potential exists to build new, productive salmon runs. Observations of five species of Pacific salmon in the Arctic date back a number of decades (Craig and Haldorson 1986). As the Arctic warms, new habitats suitable for salmon are emerging, and salmon may already be taking advantage of them (Babaluk et al. 2000). Chum and pink salmon already have self-sustaining populations in Arctic rivers, although where they spend the ice-bound Arctic winter is unknown (Irvine et al. 2009*b*). It is not yet clear that the number of viable populations of salmon in the Arctic is actually increasing (Stephenson 2006), but the capacity of salmon to invade new habitats is well known (Milner et al. 2000; Anderson and Quinn 2007). Given time, salmon will naturally colonize the Arctic as conditions there become suitable (Vermeij and Roopnarine 2008). However, their rate of finding and colonizing new habitats may be too slow to keep ahead of global warming or to beat the rush to exploit mineral and other Arctic resources (e.g., Borgerson 2008). Sockeye, in particular, tend to be among the last to colonize new habitats, and their expansion into the Arctic may lag behind other kinds of development. Managers and policy makers should be thinking now about assisting salmon to colonize the Arctic and identifying suitable habitats for protection. Otherwise, this opportunity may be lost as well.

We are entering a new era of inexorable change for salmon and their habitats. Under global climate change, we cannot assume that today's most productive populations and regions will sustain that productivity into the future. Sockeye salmon in the Fraser basin, situated near the southern limit of the species' North American distribution, is highly vulnerable to the impacts of climate change. Other sockeye stocks and other species in British Columbia are also vulnerable. Research has begun to identify policy and management tools that will help mitigate the impact of climate change (Nelitz et al. 2007, 2010; Irvine 2009), and these should be implemented to the extent possible in keeping with the wild salmon policy. It is my view, however, that these measures will be insufficient to sustain salmon production in the southern part of their range through this century. If we wish to sustain options for high salmon production in Canadian river systems, we need to begin planning for the emergence of habitats capable of producing salmon in the Arctic. Given the current enthusiasm for industrial development in a warming Arctic, it will be necessary to identify and protect the potentially most productive habitats in advance of the development of abundant salmon populations. In the Arctic, salmon policy and management will need to be highly proactive.

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